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FRUITS AND SEEDS OF THE CUNONIACEAE

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THE DICOTYLEDONOUS FAMILY Cunoniaceae consists of woody plants almost totally restricted to the Southern Hemisphere. It has long been of evolutionary interest as a putatively primitive and basal or near-basal group in the large rosalean complex from which a number of families have perhaps been derived (Dickison, 1975a). Depending upon taxonomic interpretation, it contains between 19 and 27 genera.

As pointed out by Dickison (1980b), members of the family are morphologically diverse, and considerable difference of opinion still exists regarding both generic circumscription and intrafamilial and interfamilial relationships. For example, an overall similarity in gross floral morphology has recently led Hoogland (1979) to reduce four Australasian genera to synonymy with the previously monotypic Chilean genus *Caldcluvia* D. Don and, at the same time, to establish the new segregate genus *Acsmithia* Hoogl. Within the family, Engler (1928), in his treatment for *Die Natürlichen Pflanzenfamilien*, recognized 26 genera distributed among five tribes. These five tribes have been maintained by Schulze-Menz (1964) in the most recent edition of Engler's *Syllabus*. Available evidence indicates, however, that Engler's treatment does not accurately reflect evolutionary groupings within the assemblage.

It is becoming clear, moreover, that parallel and reticulate evolution have often produced superficially similar morphologies among cunoniaceous genera. It is equally clear that the previously available morphological and anatomical data have often led to inaccurate systematic conclusions. During the past several years, I have been engaged in a thorough morphological and anatomical study of the Cunoniaceae with three main objectives: a better circumscription of the family and an eventual clarification of the interrelationships among genera of Cunoniaceae; an elucidation of the relationships of the Cunoniaceae to other families; and a better understanding of the overall patterns and trends of evolution within the family. Toward these goals, earlier research has dealt with aspects of floral (Dickison, 1975a), foliar (Dickison, 1975b), nodal (Dickison, 1980a), and wood anatomy (Dickison, 1980b). Although the resulting data

have provided further insight into the relationships and relative degrees of advancement of various taxa, additional detailed and comprehensive study of other aspects will be required in order to obtain a reasonably accurate picture of intrafamilial relationships. This paper describes the anatomy of both fruits and seeds.

The very scanty embryological information available on the Cunoniaceae has been summarized by Davis (1966). Aside from the incomplete accounts provided in numerous regional floras, little has been written concerning fruit and seed structure of the family (see Corner, 1976). More recent contributions dealing with cunoniaceous embryology and seed structure include papers by Govil and Saxena (1976) on *Weinmannia fraxinea*, Prakash and McAlister (1977) on *Bauera capitata* Ser., Krach (1977) on general seed morphology in the Cunoniaceae, and Kennedy and Prakash (1981) on *Callicoma serratifolia*. Outline drawings of seeds were provided by Bernardi (1964) in his revision of *Weinmannia*.

## MATERIALS AND METHODS

Fruits and seeds of 20 genera and close to 100 species were examined in the present study. Specimens studied are presented in TABLE 1. Preserved fruits and seeds, in various stages of maturation, were embedded in paraffin and cut on a rotary microtome. Sections were subsequently stained with a combination of safranin and fast-green. Additional seeds were gathered from mature fruits on herbarium specimens housed at A, BRI, CANB, DUKE, GH, L, NCU, NOU, and Z (herbarium acronyms according to Holmgren, Keuken, & Schofield, 1981). For scanning electron microscopy, dried seeds were affixed to stubs with double-stick tape, gold coated, and observed directly. The concept used of familial and generic limits follows Hoogland (1960, 1979, 1981). Most seed terminology follows the usage of Corner (1976). Slides are deposited in the Department of Biology, The University of North Carolina at Chapel Hill.

## OBSERVATIONS

### DEHISCENT-FRUITED GENERA

**FRUITS.** Twelve genera are characterized by dehiscent fruits: *Acrophyllum* Benth. (1 species), *Acsmithia* (14), *Bauera* Banks ex H. C. Andrews (3), *Caldcluvia* (11), *Callicoma* H. C. Andrews (1), *Cunonia* L. (ca. 20), *Geissois* Labill. (ca. 17), *Lamanonia* Vell. (6 to 8), *Pancheria* Brongn. & Gris (ca. 28), *Spiraeanthemum* A. Gray (6), *Vesselowskya* Pampan. (1), and *Weinmannia* L. (ca. 150). Fruits and seeds of *Bauera* were the only ones not examined.

In *Acsmithia* and *Spiraeanthemum* each carpel of the apocarpous gynoecia matures into a follicular fruit (FIGURE 1), while all other genera produce two- (to five-)valved, sometimes horned capsules that undergo septicidal dehiscence (FIGURES 2, 4–7). In contrast with the capsules of other genera, those of *Cunonia* dehisce by means of an acropetal separation of carpels from the persistent central column of tissue (FIGURE 3). Fruit-wall surfaces range between glabrous

TABLE 1. Specimens of Cunoniaceae examined.

| TAXON  | COLLECTOR                            | COUNTRY OF ORIGIN | VOUCHER  | FRUIT | SEED |
|--|--------------------------------------|-------------------|----------|-------|------|
| <i>Acrophyllum australe</i> (A. Cunn.) Hoogl.        | Stauffer et al. 5700                 | Australia         | A        | +     | +    |
| <i>Acsmithia densiflora</i> (Brongn. & Gris) Hoogl.  | McKee 2683                           | New Caledonia     | L        |       | +    |
|  | Dickison 220                         | New Caledonia     | NCU      | +     | +    |
|  | Musselman et al. 5222                | New Caledonia     | NCU      |       | +    |
|  | Stauffer et al. 5797                 | New Caledonia     | Z        |       | +    |
| <i>A. elliptica</i> (Pampan.) Hoogl.                 | Veillon 2844                         | New Caledonia     | NCU      |       | +    |
| <i>A. integrifolia</i> (Pulle) Hoogl.                | Brass 12693                          | New Guinea        | L        |       | +    |
| <i>A. pedunculata</i> (Schlechter) Hoogl.            | Veillon 1079                         | New Caledonia     | NOU      |       | +    |
| <i>A. pubescens</i> (Pampan.) Hoogl.                 | Schmid 431                           | New Caledonia     | NOU      |       | +    |
| <i>A. pulleana</i> (Schlechter) Hoogl.               | Brass 12017                          | New Guinea        | A, L     |       | +    |
| <i>A. reticulata</i> (Schlechter) Hoogl.             | Galore & Wood, NGF 41005             | New Guinea        | A, L     |       | +    |
| <i>A. undulata</i> (Vieill.) Hoogl.                  | Vieillard 2078                       | New Caledonia     | L        |       | +    |
| <i>Aistopetalum multiflorum</i> Schlechter           | Hoogland & Craven 10826              | New Guinea        | CANB     | +     | +    |
| <i>Anodopetalum biglandulosum</i> (Hooker) Hooker f. | Webb 3337                            | Tasmania          | BRI      | +     | +    |
| <i>Caldcluvia australiensis</i> (Schlechter) Hoogl.  | Hoogland 8538                        | Australia         | A, L     | +     | +    |
| <i>C. brassii</i> (Perry) Hoogl.                     | Brass 30592                          | New Guinea        | L        |       | +    |
|  | Brass 29616                          | New Guinea        | A        |       | +    |
|  | Hoogland 9406                        | New Guinea        | CANB     | +     | +    |
| <i>C. celebica</i> (Blume) Hoogl.                    | Hartley 12298                        | New Guinea        | L        |       | +    |
|  | Havel & Kairo, NGF 17084             | New Guinea        | A        |       | +    |
|  | Brass 3214                           | Solomon Is.       | BRI      |       | +    |
|  | Kujewski 1715                        | Bougainville Is.  | BRI      |       | +    |
| <i>C. clemensiae</i> (Perry) Hoogl.                  | Van Balgooy 969                      | New Guinea        | L        |       | +    |
| <i>C. fulva</i> (Schlechter) Hoogl.                  | Van Royen, NGF 18266                 | New Guinea        | L        |       | +    |
| <i>C. nymanii</i> (K. Schum.) Hoogl.                 | Henty et al., NGF 41525              | New Guinea        | L        |       | +    |
|  | Stevens, LAE 50443                   | New Guinea        | L        |       | +    |
|  | Hoogland & Schodde 7325              | New Guinea        | Z        |       | +    |
|  | Hoogland & Craven 11,069             | New Guinea        | L        | +     | +    |
|  | Croft & Lelean, NGF 34981            | New Guinea        | A        | +     | +    |
| <i>C. paniculata</i> (Cav.) D. Don                   | Dombey 713                           | Chile             | L        |       | +    |
|  | Eyerdam & Beetle 24618               | Chile             | GH       |       | +    |
| <i>C. paniculosa</i> (F. Mueller) Hoogl.             | Thorne et al. 25938                  | Australia         | L        |       | +    |
|  | Hoogland 1115                        | Australia         | CANB     |       | +    |
| <i>C. papuana</i> (Pulle) Hoogl.                     | Kalkman 5316                         | New Guinea        | L        |       | +    |
| <i>C. rosifolia</i> (A. Cunn.) Hoogl.                | Wilkes Exp. s.n.                     | New Zealand       | GH       |       | +    |
|  | Walker s.n.                          | New Zealand       | GH       |       | +    |
| <i>C. rufa</i> (Schlechter) Hoogl.                   | Hoogland & Pullen 6081               | New Guinea        | L        |       | +    |
|  | Hoogland & Pullen 5438               | New Guinea        | CANB     |       | +    |
| <i>Callicoma serratifolia</i> H. C. Andrews          | Hoogland 11692                       | Australia         | A, CANB  | +     | +    |
|  | Dickison & Jessup 295                | Australia         | BRI, NCU | +     | +    |
|  | White 10279                          | Australia         | A        |       | +    |
| <i>Ceratopetalum succirubrum</i> C. T. White         | Hartley 10,967                       | New Guinea        | A        | +     | +    |
|  | Croft & Marsh, LAE 71177             | New Guinea        | BRI      | +     | +    |
| <i>Codia nitida</i> Schlechter                       | Dickison 221                         | New Caledonia     | NCU      | +     | +    |
|  | Jaffre 2223                          | New Caledonia     | NOU      |       | +    |
| <i>C. obcordata</i> Brongn. & Gris                   | Guillaumin & Baumann-Bodenheim 13117 | New Caledonia     | A        |       | +    |
| <i>Cunonia atrorubens</i> Schlechter                 | Blanchon 649                         | New Caledonia     | NOU      |       | +    |

TABLE 1 (continued).

| TAXON  | COLLECTOR                               | COUNTRY OF ORIGIN | VOUCHER  | FRUIT | SEED |
|--|---|-------------------|----------|-------|------|
| <i>C. balansae</i> Brongn. & Gris                          | <u>Dickison 230</u>                     | New Caledonia     | NCU      | +     | +    |
| <i>C. capensis</i> L.                                      | <u>Lam &amp; Meeuse 4656</u>            | South Africa      | L        |       | +    |
| <i>C. lenormandii</i> Pampan.                              | <u>McKee 7975</u>                       | New Caledonia     | L        |       | +    |
| <i>C. macrophylla</i> Brongn. & Gris                       | <u>Bernardi 9507</u>                    | New Caledonia     | L        |       | +    |
|  | <u>Webster &amp; Hildreth 14493</u>     | New Caledonia     | GH       | +     |      |
| <i>C. pseudoverticillata</i> Guillaumin                    | <u>McKee 4410</u>                       | New Caledonia     | L        |       | +    |
| <i>C. pterophylla</i> Schlechter                           | <u>Dickison 238</u>                     | New Caledonia     | NCU      | +     | +    |
| <i>C. pulchella</i> Brongn. & Gris                         | <u>Dickison 287</u>                     | New Caledonia     | NCU      | +     | +    |
|  | <u>Dickison 218</u>                     | New Caledonia     | NCU      | +     | +    |
| <i>C. purpurea</i> Brongn. & Gris                          | <u>Dickison 156</u>                     | New Caledonia     | NCU      | +     | +    |
|  | <u>Dickison 144</u>                     | New Caledonia     | NCU      |       | +    |
| <i>C. schinziana</i> D#niker                               | <u>McKee 23112</u>                      | New Caledonia     | NOU      |       | +    |
| <i>Geissois benthamiana</i> F. Mueller                     | <u>Forest Guard,<br/>Lismore 3.1909</u> | Australia         | L        |       | +    |
| <i>G. biagiana</i> (F. Mueller) F. Mueller                 | <u>Dockrill 34</u>                      | Australia         | L        |       | +    |
| <i>G. hippocastaneifolia</i> Guillaumin                    | <u>Dickison 284</u>                     | New Caledonia     | NCU      | +     | +    |
| <i>G. pruinosa</i> Brongn. & Gris                          | <u>Dickison 217</u>                     | New Caledonia     | NCU      | +     | +    |
| <i>G. stipularis</i> A. C. Sm.                             | <u>Fiji Herb. 31297</u>                 | Fiji              | NCU      | +     | +    |
| <i>Gillbeea papuana</i> Schlechter                         | <u>Brass 31815</u>                      | New Guinea        | A        | +     | +    |
| <i>Lamanonia ternata</i> Vell.                             | <u>Irwin et al. 8603</u>                | Brazil            | GH       |       | +    |
| <i>L. tomentosa</i> (Cambess.) O. Kuntze                   | <u>Balansa 4752</u>                     | Paraguay          | L        |       | +    |
| <i>Pancheria confusa</i> Guillaumin                        | <u>Veillon 66</u>                       | New Caledonia     | NOU      |       | +    |
| <i>P. elegans</i> Brongn. & Gris                           | <u>Dickison 158</u>                     | New Caledonia     | NCU      | +     | +    |
| <i>P. hirsuta</i> Vieill.                                  | <u>Dickison 227</u>                     | New Caledonia     | NCU      | +     | +    |
| <i>P. reticulata</i> Guillaumin                            | <u>Bernardi 12768</u>                   | New Caledonia     | Z        |       | +    |
| <i>P. robusta</i> Guillaumin                               | <u>Dickison 248</u>                     | New Caledonia     | NCU      | +     | +    |
| <i>P. sebertii</i> Guillaumin                              | <u>Franc 2109</u>                       | New Caledonia     | A        |       | +    |
| <i>Platylophus trifoliatus</i> (Thunb.) D. Don             | <u>Bolus 621</u>                        | S. Africa         | A        | +     | +    |
|  | <u>Wicht 460/461</u>                    | S. Africa         | L        |       | +    |
| <i>Pseudoweinmannia lachnocarpa</i><br>(F. Mueller) Engler | <u>Clemens 43294</u>                    | Australia         | A        | +     | +    |
| <i>Pullea glabra</i> Schlechter                            | <u>Brass 31156</u>                      | New Guinea        | A        | +     | +    |
| <i>P. stutzeri</i> (F. Mueller) Gibbs                      | <u>Irvine 1253</u>                      | Australia         | BRI      |       | +    |
| <i>Schizomeria ilicina</i> (Ridley) Schlechter             | <u>Brass 12150</u>                      | New Guinea        | A        | +     |      |
| <i>S. ovata</i> D. Don                                     | <u>Hoogland 11684</u>                   | Australia         | CANB     | +     | +    |
|  | <u>Dickison &amp; Jessup 297</u>        | Australia         | BRI, NCU | +     | +    |
| <i>S. whitei</i> Matff.                                    | <u>Dickison 205</u>                     | Australia         | NCU      | +     | +    |
| <i>Spiraeanthemum katakata</i> Seem.                       | <u>A. C. Smith 4371</u>                 | Fiji              | A        |       | +    |
|  | <u>A. C. Smith 4409</u>                 | Fiji              | L        |       | +    |
| <i>S. macgillivrayi</i> Seem.                              | <u>Morrison 25.6.1896</u>               | New Hebrides      | A        | +     |      |
| <i>S. samoense</i> A. Gray                                 | <u>Bristol 2136</u>                     | Samoa             | L        |       | +    |
| <i>Vesselowskyia rubifolia</i> (F. Mueller) Pampan.        | <u>White 11482</u>                      | Australia         | A        |       | +    |
|  | <u>Schodde 3210</u>                     | Australia         | CANB     | +     | +    |
|  | <u>Herb. D'Alleizette 2151</u>          | Australia         | L        |       | +    |
| <i>Weinmannia affinis</i> A. Gray                          | <u>A. C. Smith 7608</u>                 | Fiji              | L        |       | +    |
| <i>W. aphanoneura</i> Airy Shaw                            | <u>Ashton, BRUN 1044</u>                | Borneo            | L        |       | +    |
| <i>W. bangii</i> (Rusby) Pampan.                           | <u>Buchtien s.n.</u>                    | Bolivia           | L        |       | +    |

TABLE 1 (continued).

| TAXON  | COLLECTOR                             | COUNTRY OF ORIGIN       | VOUCHER | FRUIT | SEED |
|--|---------------------------------------|-------------------------|---------|-------|------|
| <i>W. blumei</i> Planchon                    | Dickison 215                          | New Guinea              | NCU     | +     | +    |
|  | Koorders 7647B                        | Java                    | L       |       | +    |
|  | Schmutz 4588                          | Lesser Sunda Is.        | L       |       | +    |
| <i>W. celebica</i> Koord.                    | Van Balgooy 3809                      | Celebes                 | L       |       | +    |
| <i>W. clemensiae</i> Steenis                 | J. & M. S. Clemens 50877              | Borneo                  | L       |       | +    |
| <i>W. decora</i> Tul.                        | Bernardi 11961                        | Madagascar              | L, Z    |       | +    |
| <i>W. denhamii</i> Seem.                     | Bernardi 13258                        | New Hebrides            | L       |       | +    |
|  | Bernardi 12986                        | New Hebrides            | P       |       | +    |
| <i>W. descombesiana</i> Bernardi             | Eyma 3590                             | Celebes                 | L       |       | -    |
| <i>W. dichotoma</i> Brongn. & Gris           | Bernardi 12616                        | New Caledonia           | Z       |       | +    |
| <i>W. fraxinea</i> (D. Don) Miq.             | Forman 51                             | Cult., Java             | L       |       | +    |
| <i>W. glabra</i> L.                          | Lansberger s.n.                       | Venezuela               | L       |       | +    |
| <i>W. hutchinsonii</i> Merr.                 | Mendoza, PNH 18409                    | Philippines             | L       |       | +    |
| <i>W. luzoniensis</i> Vidal                  | Gacad, FB 27274                       | Philippines             | BO      |       | +    |
| <i>W. mauritiana</i> D. Don <sup>1</sup>     | D'Alleizette 2166                     | Réunion                 | L       |       | +    |
| <i>W. monticola</i> Daniker                  | McKee 23892                           | New Caledonia           | NOU     |       | +    |
| <i>W. negrosensis</i> Elmer                  | Ramos, Philippine Plants<br>1287      | Philippines             | L       |       | +    |
| <i>W. paitensis</i> Schlechter               | Bernardi 9881                         | New Caledonia           | L       |       | +    |
| <i>W. parviflora</i> Forster                 | Gillett 2215                          | Marquesas Is.           | L       |       | +    |
| <i>W. pinnata</i> L.                         | Sousa & Rico 8118                     | Mexico                  | NCU     |       | +    |
| <i>W. pullei</i> Schlechter                  | Hoogland & Schodde 7242               | New Guinea              | Z       |       | +    |
| <i>W. purpurea</i> Perry                     | Kajewski 1738                         | Solomon Is.             | L       |       | +    |
| <i>W. racemosa</i> L. f.                     | Philipson et al. 349<br>Dickison s.n. | New Zealand<br>Cult., E | NCU     | +     | +    |
| <i>W. richii</i> A. Gray                     | A. C. Smith 6813                      | Fiji                    | L       |       | +    |
| <i>W. rubrinervis</i> Ettingsh. <sup>2</sup> | D'Alleizette s.n.                     | Madagascar              | L       |       | +    |
| <i>W. serrata</i> Brongn. & Gris             | Bernardi 12816                        | New Caledonia           | L       |       | +    |
| <i>W. subsessiliflora</i> Ruiz & Pavon       | Vasquez A130                          | Peru                    | DUKE    |       | +    |
| <i>W. sylvicola</i> A. Cunn.                 | Van Steenis 22314                     | New Zealand             | L       |       | +    |
| <i>W. tannaensis</i> Guillaumin              | Bernardi 12909                        | New Hebrides            | L, Z    |       | +    |
| <i>W. tinctoria</i> Sm.                      | Bernardi 14516                        | Réunion                 | Z       |       | +    |
| <i>W. trichophora</i> Perry                  | Pullen 374                            | New Guinea              | L       |       | +    |
| <i>W. trichosperma</i> Cav.                  | Zollner 3137                          | Chile                   | L       |       | +    |
| <i>W. vescoi</i> Drake                       | Van Balgooy 1796                      | Tahiti                  | L       |       | +    |

<sup>1</sup>Syn. *W. biviniana* Tul.<sup>2</sup>Syn. *W. rutenbergii* Engler.

and tomentose. The calyx is either persistent or deciduous in the fruit, with both of these character states sometimes present within a single genus (e.g., *Weinmannia*).

All of the plants have mature pericarps that are differentiated into an outer parenchymatous region and an inner region of rigid, thick-walled, and highly lignified cells (FIGURES 19, 20, 22). The endocarp tissue is thicker along the

dorsal wall and becomes thinner in ventral regions. In older fruits of *Cunonia*, the endocarp may become separated from the outer parenchymatous layers. The lignified valve margins, which represent the halves of the original septa, are illustrated in FIGURES 2 and 5. Pericarp thickness ranges from a low of four to eight cells (*Weinmannia*) to a high of 30 to 40 cells (*Geissois*). Fruit vasculature mirrors the pattern of gynoecial venation (Dickison, 1975a), although in the mature fruit veins become ensheathed by sclerenchyma.

Epidermal cells of the outer surface of the pericarp are generally rectangular in transection, with a moderately thick cuticle on the outside. *Weinmannia racemosa* has a conspicuously striate external pattern. Mature fruits of *Cunonia pulchella* are covered with six or seven layers of periderm and have scattered lenticels. The parenchymatous central region of the pericarp is composed of isodiametric cells that may become moderately thick walled in older fruits. Numerous brachysclereids are present in the mesocarp. Scattered "mucilaginous idioblasts" with frothy contents occur in *C. balansae*, *C. pterophylla*, *Geissois hippocastaneifolia*, and *Pancheria confusa*. Druses are common in *Cunonia balansae*, *C. capensis*, *C. pterophylla*, and *Pancheria robusta*. In *Acsmithia densiflora*, *Caldcluvia rosifolia*, *Geissois pruinosa*, *Pancheria gatopen sis* Vieill. ex Guillaumin, and *Vesselowskya rubifolia* such crystals are confined to the boundary cells between outer parenchyma and endocarp or to the septum. In some species of *Cunonia*, zonation is indicated in the parenchymatous region of the pericarp by peripheral cells that stain more darkly.

The inner, multiseriate sclerenchymatous region of the fruit wall, which becomes prominent following fertilization, is composed of two distinct zones of variable thickness in which the elongated cells are oriented in opposite planes: cells of the outer zone are arranged with their long axes parallel to the long axis of the fruit, while those of the inner zone are at right angles.

DEVELOPMENT OF THE SEED COAT. Seed coats at early stages of development were examined for a number of capsular cunoniaceous taxa, including *Cunonia balansae* (FIGURE 131) and *Pancheria robusta* (FIGURE 134). Mature ovules are anatropous, bitegmic, and as far as is known, crassinucellate (Davis, 1966). At an early stage of seed-coat development, the outer integument is composed of a tanniferous outer epidermis and one or two subdermal layers consisting of smaller, nucleated, less densely staining cells. The outer epidermis of the inner integument gradually becomes transformed into a sclerotized exotegmen in the mature seed coat; during early stages of development, this layer is composed of rather small, nontanniferous cells with prominent nuclei (FIGURES 131, 134). Although distinction between outer and inner integuments is typically lost in the mature seed coat, examination of developmental stages during seed-coat maturation shows that seeds of the Cunoniaceae are exotegmic (*sensu* Corner, 1976); that is, the outer epidermis of the inner integument differentiates into the mechanical layer. The middle two to four layers of the inner integument, some of which may arise by secondary periclinal divisions, consist of comparatively enlarged, nontanniferous or tanniferous cells that are often tangentially flattened. Additional layers may develop along the seed edges. The inner epidermis is typically made up of densely cytoplasmic, tannin-accumulating

cells that undergo little enlargement. In older seeds the inner epidermis always stains very darkly (FIGURE 133).

**MATURE SEEDS.** The taxonomic literature indicates that seeds range in length from small (ca. 0.4 mm) to relatively large (ca. 6 mm). I have found no exceptions to these dimensions. Outline varies from narrowly elliptic to elliptic or lanceolate. Angular seeds occur in *Cunonia* (FIGURES 44, 51). Seed numbers range from one to many per locule, with ovule abortion common (FIGURES 130, 132). In cunoniaceous seeds the major features that show significant variation and that may be combined in different ways are type and distribution of epidermal appendages, shape and wall characteristics of epidermal cells, and occurrence, type, and abundance of warts and striations. Seed coats are either glabrous or papillate (tuberculate), and appendages are usually present in the form of wings or hairs. A hilar scar is clearly visible in most taxa (FIGURE 91), and an elongate raised raphe is generally present. Seeds are supplied by a single undivided raphal bundle (FIGURE 135). A straight embryo is always embedded in abundant starchy endosperm (FIGURES 135, 136).

Wings occur on seeds of all examined specimens of *Acsmithia*, *Callicoma*, *Cunonia*, *Geissois*, *Lamanonia*, *Pancheria*, *Spiraeanthemum*, and *Vesselowskyia*, as well as on those of some specimens assigned to the genus *Caldcluvia*. Wings are without vasculature and vary in size, shape, and location. Those of *Geissois* are long, flattened structures confined to an upper terminal position on the seed (FIGURE 37). The same condition is found in some species of *Pancheria*, such as *P. confusa* (FIGURES 31, 32), and in *Acsmithia vitiense* (A. Gray) Hoogl. Terminal wings attached both chalazally and micropylarly—and also sometimes laterally—occur in *Acsmithia*, *Caldcluvia*, *Cunonia*, *Lamanonia*, *Spiraeanthemum*, *Vesselowskyia rubifolia*, and some species of *Pancheria* (FIGURES 33, 39, 46, 49, 52, 55, 57, 58, 65, 71, 73, 81). When both distal and basal wings are present, the two often differ in length and shape. In a number of species of *Acsmithia*, *Cunonia*, *Lamanonia*, and *Pancheria*, wings sometimes extend along one or both sides of the seed body as lateral appendage(s) (FIGURES 35, 39, 49, 51, 55). Such lateral wings may extend up to the entire length of the seed body and appear always to form on the hilar side. Wing size and shape are also quite variable, ranging from rather long, broad structures with rounded apices, to triangular, to short, narrow outgrowths. Structurally mature wings consist primarily of two epidermal layers; between these one to three layers of unorganized or crushed cells may occur.

Hairy seeds characterize the large and widely distributed genus *Weinmannia* and the New Zealand and Australian species of *Caldcluvia*—*C. australiensis* (FIGURE 61), *C. paniculosa* (FIGURE 67), and *C. rosifolia* (FIGURE 62). Three principal patterns of hair distribution are present: scattered, sparsely distributed, not confined to the ends of seeds (FIGURES 61, 62, 67, 87, 91, 102, 105, 112); in tuft restricted to the ends of seeds (FIGURES 83, 85, 88, 97, 100, 103, 106, 109); and abundant over the entire seed surface (FIGURES 92, 96). Intermediate conditions exist in which seeds are predominantly apically comate, with hairs also occasionally present on the sides (FIGURE 108). Great variation also occurs in hair length and abundance, with seeds ranging from sparsely

hirsute in *W. tinctoria* (FIGURE 91), *W. trichosperma* (FIGURE 112), and *W. bangii*, to very tomentose in such species as *W. pullei* (FIGURE 92) and *W. rubrinervis* (FIGURE 96). In *W. richii* tufts of long hairs are present at both ends of the seed, and short, almost papillalike hairs are scattered over the sides (FIGURES 94, 95). Seed hairs are simple, unicellular, sometimes striate, thin-walled structures without specialized ends such as hooks or barbs and are typically curved and intertwined in the mature seed.

Surface features of seeds belonging to this group of genera are likewise quite variable. Species differ not only in the more readily visible aspects of epidermal cell shape, size, outline, and wall characteristics, but also in the less conspicuous secondary features of external wall ornamentation. External epidermal cell walls are smooth, striate, warty, or a combination of striate and warty. Narrow cuticular striations mostly parallel with the long axes of epidermal cells have been observed in *Acsmithia elliptica*, *Acrophyllum australe* (FIGURE 80), *Caldcluvia celebica* (FIGURE 60), *Callicoma serratifolia* (FIGURE 78), and many species of *Weinmannia* such as *W. decora*, *W. dichotoma*, *W. pullei*, *W. tannaensis*, *W. trichosperma*, *W. richii*, and *W. purpurea* (FIGURES 84, 93, 113, 120). More or less irregularly oriented striations occur in *Cunonia macrophylla*, *Geissois biagiana*, *Caldcluvia fulva*, and *C. papuana* (FIGURES 43, 48, 70, 72). Striations vary considerably in size and abundance (compare FIGURES 111 and 113). A warty external surface has been noted in *Cunonia purpurea*, *Vesselowskyia rubifolia*, *Weinmannia blumei*, *W. pinnata*, *W. subsessiliflora*, *W. negrosensis*, *W. hutchinsonii*, *W. descombesiana*, and *W. celebica* (FIGURES 45, 82, 104, 116, 117). Some species such as *W. affinis*, *W. monticola*, *W. serrata*, *W. sylvicola*, *W. luzoniensis*, *W. fraxinea*, *W. vescoi*, and *W. denhamii* (FIGURES 89, 98, 99, 101, 111, 114, 119) have both warts and striae. Warts vary in size and prominence and range in outline from circular (most commonly) to angular to sometimes rectangular (in *W. luzoniensis*, FIGURE 101).

A markedly papillate (tuberculate) condition, due to the unicellular protrusions of epidermal cells, distinguishes *Acrophyllum australe* (FIGURE 79) and *Callicoma serratifolia* (FIGURE 76), as well as *Caldcluvia brassii*, *C. paniculata* (FIGURE 64), *C. papuana* (FIGURE 69), *C. nymanii* (FIGURES 73, 74, 135), *C. clemensiae* (FIGURE 66), and *C. celebica* (FIGURES 58–60). Hoogland (1979) has drawn attention to the fact that among species of *Caldcluvia*, only the mature seed wall is papillate. Seeds of *Acrophyllum* are unique in being completely covered by papillae (FIGURE 79). Each papilla is generally broad and flattened at the base, smooth at the apex, and with a striate cuticle on the sides (FIGURE 80). Although the papillae of *Caldcluvia* are morphologically similar, they are scattered and cover the seed coat incompletely (FIGURES 59, 64, 66). As in *Acrophyllum*, the papillae are flattened at the base, rounded apically, and striate, differing only in that the striae extend over the apex (FIGURE 60). *Callicoma serratifolia* also produces papillate or tuberculate seeds with striate papillae (FIGURE 78). This observation is in agreement with that of Kennedy and Prakash (1981).

Scanning electron micrographs show that species of *Pancheria* have a distinctive seed surface in which enlarged epidermal cells of various outlines, with smooth, rounded outer walls, are arranged in mosaic patterns. These prominent



epidermal cells may completely cover the surface of both the wing and the seed body, as in *P. elegans* (FIGURES 35, 36), or they may be scattered over the seed surface along with less prominent cells of irregular outline, as in *P. sebertii* (FIGURE 34). Similar enlarged cells occur in *Cunonia schinziana* (FIGURE 50) and *C. macrophylla* (FIGURE 47). The surface of *C. purpurea* seeds, however, is composed of irregularly polygonal cells with thin, slightly raised lateral walls. Cells of irregular outline with moderately thick to thin lateral walls comprise the seed coats of *Lamanonia* (FIGURES 39, 40) and *Geissois stipularis* (FIGURES 37, 38). The Australian species of *Geissois* have diagnostic surface patterns: the epidermal cells of *G. benthamiana* seeds have raised outer walls covered with an unorganized arrangement of pits and irregular ridges and grooves (FIGURES 41, 42), while those of *G. biagiana* seeds have dome-shaped outer walls covered with prominent striations that are oriented at a flat to steep angle in relation to the inner walls (FIGURE 43). Narrowly rectangular surface cells with moderately thick and slightly raised lateral walls extending parallel with the long axis of the seed are present in *Vesselowskya rubifolia* (FIGURE 82). Structurally complex epidermal cells distinguish seeds of *Callicoma serratifolia*. These cells are thick walled and have a combination of thick surface ridges and striae forming intricate patterns of the type seen in FIGURE 77.

The seed-coat surface of *Spiraeanthemum katakata* and *S. samoense* generally has smooth, thin-walled, rectangular cells that tend to be without conspicuously raised anticlinal walls and are oriented with their long axes parallel to the long axis of the seed (FIGURE 53). *Acsmithia elliptica*, *A. densiflora*, *A. integrifolia*, and *A. pulleana* have a microreticulate sculpturing of small, square or rectangular to elongate cells with moderately thick, raised lateral walls (FIGURES 54, 56). It is particularly interesting that in some collections of *Acsmithia*, the surface pattern on the seed body is structurally different from that on the wings. In the taxa examined, surface cells on the wings are irregularly oriented, often interwoven, and fibrous looking—distinctly different in appearance from those on the body (FIGURES 54, 55). This feature has not been observed in other cunoniaceous genera.

The genus *Caldcluvia* includes plants with diverse surface features. In addition to the papillate condition described previously, the winged seeds of such species as *C. brassii* and *C. paniculata* have irregularly rectangular, hexagonal, or polygonal epidermal cells. Among the New Guinean species, *C. nymanii* appears distinctive in lacking obvious surface striations (FIGURE 75). *Caldcluvia australiensis*, *C. rosifolia*, and *C. paniculosa*—species with hairy seeds—have surface cells with raised and irregularly undulate anticlinal walls (FIGURES 62, 63, 68, 69).

Seed-surface patterns in *Weinmannia* are the most diverse in the family. In addition to the diversity discussed earlier, presence and distribution of striations and warts, and epidermal cell shape and wall characteristics are also quite variable. A reticulate surface composed of irregularly polygonal cells with moderately thick and raised radial walls occurs in *W. pinnata* (FIGURE 90) and *W. subsessiliflora* (FIGURE 87). A more irregular pattern of rectangular cells, in places approaching a rugulate condition, occurs in *W. decora* (FIGURE 120) and *W. tinctoria* (FIGURE 91). Vertically elongate cells of somewhat irregular outline

are present in a number of species. Variations in the appearance of this condition are illustrated in FIGURES 86, 107, and 118. In FIGURE 86 fine bars can be seen connecting the parallel ridges. A series of low, rounded ridges interspersed with small, spherical or polygonal warts is characteristic of *W. monticola* (FIGURE 89). The seed-coat surface of *W. tannaensis* consists of a series of undulating, usually longitudinally extended, low ridges and valleys (FIGURE 84); two ridges lying in close proximity are often connected by strands of wall material. The most common surface pattern in *Weinmannia* seeds is one of vertically elongated epidermal cells with raised, undulate anticlinal walls (FIGURES 95, 97, 102, 106, 107, 114–117). Low, irregularly undulating ridges are present in *W. luzoniensis*, *W. fraxinea*, and *W. denhamii* (FIGURES 101, 110, 111, 119). These ridges vary in height and width.

Histologically, the mature seed coat in these genera is composed of a cuticle and (four or) five (or more) layers of cells (FIGURES 23–26, 28). Four layers distinguish both *Acrophyllum australe* (FIGURE 30) and *Callicoma serratifolia*, whereas between six and eight cell layers characterize *Geissois*. This results in a three-layered testa and a one-, two-, or many-layered tegmen. Epidermal cells are cutinized, thin- or moderately thick-walled, and rectangular in transection. Surface cells in *Geissois* and *Pancheria* are typically enlarged and are often radially elongated as viewed in transection, with curved or dome-shaped outer walls (FIGURES 41, 42). In fully mature seeds of *Geissois*, the enlarged epidermal cells covering the wings may become very thick walled and sclerotic. Similarly enlarged cells also occur on the surface of some *Cunonia* seeds. The subepidermal layer is composed of rectangular or compressed, thin-walled, nonlignified cells. Among species examined, *Acrophyllum australe*, *Caldcluvia rosifolia*, *Cunonia pulchella*, *Geissois stipularis*, *Pancheria confusa*, *P. gatopensis*, and *Vesselowskyia rubifolia* have a crystalliferous hypodermis (FIGURES 25, 28). Each crystal cell contains a solitary, angular crystal, although infrequent druses were observed in *G. stipularis*. Beneath the hypodermis a single layer of thick-walled, lignified, sclerotic cells is present in all taxa. These cells compose the only mechanical layer of the seed coat and are oriented longitudinally. Some variation exists among genera with regard to the shape and type of wall thickening of the sclerenchymatous cells as viewed in transection. While sclerenchyma cells are most commonly cuboidal or shortly radially elongate, with moderately thick walls, those of *Vesselowskyia rubifolia* are small in diameter and have very thick walls (FIGURE 28). Seeds of *Acsmithia densiflora* (FIGURES 23, 136), *Caldcluvia rosifolia*, and *Weinmannia racemosa* have a sclerotic layer composed of cells with thickened inner and radial walls (U-shaped thickenings). Cells that are circular in transectional outline and have very thick walls occur in *Acrophyllum australe* (FIGURE 30). The tegmen consists of thin-walled, rectangular or compressed (crushed) cells, with the innermost layer always filled with a darkly staining substance.

#### INDEHISCENT-FRUITED GENERA

Nine genera are characterized by indehiscent fruits: *Aistopetalum* Schltr. (2 species), *Anodopetalum* A. Cunn. ex Endl. (1), *Ceratopetalum* J. E. Sm. (6),

*Codia* J. R. Forster & J. G. A. Forster (ca. 10), *Gillbeea* F. Mueller (2), *Platylophus* D. Don (1), *Pseudoweinmannia* Engler (2), *Pullea* Schltr. (3), and *Schizomeria* D. Don (ca. 18).

The fruits of these genera range from indehiscent capsules, drupes, and berries to the winged fruits of *Gillbeea* (FIGURES 8–14). Seed structure is also quite variable. I have found it most convenient, therefore, to describe each genus or group of genera individually.

The most common fruit type is an indehiscent, unilocular or bilocular capsule, characteristic of *Ceratopetalum*, *Codia*, *Pseudoweinmannia*, and *Pullea*. Fruits of *Ceratopetalum*, *Codia*, and *Pullea* may be derived from gynoecea with inferior or half-inferior ovaries, resulting in a fruit wall that is partially of hypanthial origin. Fruits of *Ceratopetalum* are bilocular, one- or two-seeded, and surrounded by enlarged, stellately spreading sepals (FIGURE 11). Up to four seeds occur in *Codia* and *Pseudoweinmannia* fruits, but only a single fertile one may be present in those of *Pullea glabra* var. *glabra*. Mature fruit walls range from glabrous to densely tomentose, as in *Codia* (FIGURE 14) and *Pseudoweinmannia*, respectively (FIGURES 12, 13).

Pericarps of *Ceratopetalum* and *Pullea* are differentiated into outer exocarp, middle mesocarp, and inner fibrous endocarp. Internal to the epidermis is a chiefly parenchymatous middle region that, in both genera, contains scattered brachysclereids. The sclereids in *P. glabra* are thin walled, whereas those in *C. succirubrum* are conspicuously thick walled and pitted. Enlarged "mucilage" cells are also present in *Pullea*. The generally narrow, fibrous, lignified endocarp is composed of thick-walled elements arranged in two zones, one oriented vertically and the other horizontally. Immediately external to the inner sclerenchymatous region in fruits of *Ceratopetalum* is a uniseriate prismatic layer in which each cell contains a solitary angular crystal.

The pericarp of *Pseudoweinmannia* also contains a prominent crystalliferous layer outside the lignified, multiseriate inner zone composed mostly of tangentially elongated fibrous cells. Mature fruits of *Pseudoweinmannia* develop characteristic placental proliferations that, at maturity, may largely fill the locules between seeds (FIGURE 21). Proliferations appear to be derived from the inner pericarp wall as well as from the placentae and have a folded appearance in sectional view; the seeds are situated between the folds. The placentae are composed of thin-walled parenchyma cells, although the lateral peripheral regions consist of two or three layers of moderately thick-walled elements that resemble endocarp tissue. The outer surface of the placenta is composed of one or two layers of conspicuously enlarged, elongated cells that are oriented radially.

The capsule wall of *Codia nitida* is composed of an outer layer of small, irregularly shaped epidermal cells and one to three layers of larger, moderately thick-walled hypodermal cells. Internal to the hypodermis is an interrupted ring of very thick-walled fibrous cells, some of which may surround the fruit vasculature. The inner half of the pericarp is constructed of loosely arranged aerenchyma, but a distinct sclerenchymatous endocarp is absent (FIGURES 144, 145).

Seeds of *Codia* and *Pullea* tend to be rather small (less than 1 mm long) and

are more or less narrowly ellipsoid to ellipsoid (FIGURES 121, 123, 124). *Pseudoweinmannia* produces slightly larger, spheroidal seeds with a somewhat lobed appearance (FIGURE 125). Seeds of *Codia* and *Pullea* are essentially without wings, although rudimentary terminal wings can be recognized in some specimens. Arillike appendages characterize seeds of *Pseudoweinmannia lachnocarpa*. These appear as a ring of rather small, distinct, localized outgrowths from the exostomal region of the testa (FIGURE 126). In the absence of developmental observations, the origin and function of these structures is uncertain, although the overall structure has the general appearance of an elaiosome.

The surface of *Pseudoweinmannia* seeds is smooth, composed of nonornamented epidermal cells with a polygonal outline (FIGURE 125). Seeds of *Codia nitida*, *C. obcordata*, *Pullea glabra* var. *glabra*, and *P. stutzeri* have a reticulate external surface composed of cells with moderately raised anticlinal walls and a polygonal or, more commonly, reticulate outline (FIGURE 122). Fine striations can be observed on the surface of *C. nitida*.

Seed coats of *Codia* and *Pullea* are thin and undifferentiated. Pigmented outer and inner epidermal layers bound a central region of one or two layers of thin-walled cells. Mechanical cells are absent (FIGURE 29). Outer epidermal cells have irregular outlines and outer walls that are dome shaped in transection. Seeds of *Codia* are supplied by a tenuous, undivided vascular bundle extending to the chalazal region, while those of *Pullea glabra* have a single bundle that subdivides and terminates within the chalaza.

In contrast with the seed coats of the two previous genera, those of *Pseudoweinmannia lachnocarpa* are composed of multiple layers with a centrally positioned zone of mechanical cells. Very enlarged outer epidermal cells lack tannin and in the apical regions of the seed are often radially elongated to the surface; epidermal cells typically have thickened outer and radial walls. Beneath the epidermis are two layers of thin-walled cells of irregular size and shape. Internal to this hypodermis is a uniseriate zone of small, relatively thin-walled, mechanical cells. The multiple tegmen is composed of approximately seven or eight layers, including the inner, tanniferous epidermis. Seeds are vascularized by a single bundle that terminates within the chalazal region and shows no evidence of branching.

Seed coats of *Ceratopetalum succirubrum* (FIGURE 27) develop a thick-walled outer layer of pigmented cells that are rectangular in transectional outline and covered by a cuticle. Beneath the epidermis are two or three layers of pigmented cells, including a layer containing large, scattered, prismatic crystals. The crystalliferous layer overlies a well-developed uniseriate region of sclerenchyma. The fibrous sclerenchymatous elements are of variable width and outline but are generally rather wide with very thick, lignified, pitted walls. The remaining tegmen contains five or six indistinct layers of compressed and pigmented cells. I was not able to interpret the pattern of seed vasculature from the material at hand.

The genus *Schizomeria* is characterized by ellipsoid to ovoid, one-locular, one-seeded, drupaceous fruits (FIGURES 8, 141). The pericarp is strongly differentiated into an outer exocarp, an extensive fleshy mesocarp, and an inner stony endocarp. The relatively thin exocarp is composed of a surface layer of

small, rectangular, thick-walled epidermal cells and a single hypodermal layer consisting of more or less rectangular thick-walled cells. The fleshy mesocarp contains very thin-walled parenchyma interspersed with numerous isolated brachysclereids and sclereid nests. Sclereids are thick-walled, highly pitted, and occasionally crystalliferous with a solitary druse in the cell lumen. The endocarp is constructed of interwoven, tangentially elongated fibrous elements. Numerous small prismatic crystals are present throughout the inner mesocarp and endocarp. Major vascular bundles are confined to the fleshy mesocarp.

The seed coat is tightly compressed against the inner pericarp wall, with the outer seed surface containing narrow grooves and ridges (FIGURE 129). Beneath a cuticular layer, the testal epidermis is composed of darkly staining cells that are mostly square in transection. Cells in the two subepidermal layers are rectangular and thin walled. Beneath the bilayered hypodermis is a distinctive uniseriate zone of columnar mechanical cells with unevenly thickened walls resembling hourglass cells (FIGURE 142). Immediately internal to the sclerenchymatous layer are one or two layers of small crystalliferous cells. These cells merge with the multiple-layered tegmen mesophyll that is derived by periclinal division in the fertilized ovule and is composed of at least 20 layers of enlarged, very thin-walled cells. Inner epidermal cells are rectangular in outline and very tanniferous (FIGURE 141). A single large raphe bundle subdivides near the chalazal end of the seed into a system of veins that terminates at the chalaza.

Fruits of *Aistopetalum* are four- to six-loculate, ovoid drupes. Each locule potentially contains a single oblong, pendulous seed (FIGURES 137, 138). Mature fruits of *A. viticoides* Schltr. average 20 mm in length and 13 mm in diameter, with seeds about 6 mm long (Hoogland, 1960).

Two immature fruits of *Aistopetalum multiflorum* were sectioned; these were 6 mm in diameter and 8 mm in length. The immature pericarp of the fruits is differentiated into exocarp, mesocarp, and endocarp on the basis of cell shape and differential retention of stain. The epidermis of the uneven outer surface of the pericarp, composed of small, rather irregularly shaped cells, is covered by a thin layer of cuticle. The hypodermis consists of five to seven layers of small cells with slightly thickened walls. The major portion of the pericarp contains isodiametric parenchyma cells of various sizes. Cells of the inner mesocarp are densely tanniferous. While immature, the endocarp is distinguished by highly tanniferous tissue (FIGURE 139). As the fruit matures, seven to ten layers of tangentially elongated elements adjacent to the locules become relatively thick walled and differentiate into a very hard endocarp. Crystals are absent from the pericarp in my material.

The immature seed coat is tightly compressed against the endocarp wall. The outer epidermis is densely pigmented and is composed of cells that are more or less square or rectangular in transectional outline. The remaining testa is generally made up of six to eight layers of tanniferous, isodiametric, thin-walled cells. A uniseriate layer composed of cells having very narrow diameters, angular outlines, and moderately thick walls separates testa and tegmen. The multiple-layered tegmen consists of six to eight layers of large, thin-walled cells that are often radially aligned, as well as an inner, tanniferous epidermis. Crystals are absent from the seed coat. A single vascular bundle enters the seed,

extends through the parenchymatous testa (FIGURE 139), and branches freely within the chalazal region to form numerous veins that become arranged within the chalazal end of the seed (FIGURE 140).

The third genus with fleshy fruits is *Anodopetalum*. The pericarp of *Anodopetalum*, in contrast with those of *Schizomeria* and *Aistopetalum*, is unlig-nified and not strongly differentiated. The fruit is therefore a berry. An outer exocarp is characterized by a layer of small, rectangular epidermal cells and up to six subepidermal layers of collenchyma. An extensive mesocarp contains parenchymatous cells and numerous scattered, highly pitted, relatively thin-walled brachysclereids. Vasculature is confined to the middle zone and, as in other fleshy fruit types of the Cunoniaceae, is not associated with ensheathing sclerenchyma. The inner pericarp region lacks sclerenchyma but is recognizable by a ring of crystalliferous cells containing acicular, clustered crystals that are accompanied by small, irregular, angular forms (FIGURE 143). The acicular crystals are more or less needlelike but have blunt ends, so they are somewhat intermediate between raphides and styloids.

In my reexpanded material the seed coat is not well preserved, but it can be determined to be parenchymatous and to consist of more than ten cell layers. Epidermal cells are irregular in outline and often have dome-shaped outer walls. A distinct layer of sclerenchyma is absent. As in the other cunoniaceous genera with fleshy fruit, seeds are vascularized by a single vein that divides repeatedly in the lower half of the seed before ending within the chalaza.

The indehiscent trilocular fruit of *Gillbeea* has three prominent wings that extend the length of the central fruit column and are formed by the lateral expansion of the carpel wall (FIGURES 10, 15). Hoogland (1960) described the carpels as each containing a single seed, although only one fertile locule existed in each of the two fruits sectioned for this study (FIGURE 15).

The wings have a prominent reticulate venation, which in mature fruits is surrounded by massive sclerenchymatous sheathing. The pericarp is composed of small epidermal cells, a parenchymatous mesocarp, and a narrow, two- or three-layered endocarp composed of fibrous elements, which is separated from the parenchymatous outer region by a crystalliferous layer containing angular crystals.

Seeds of *Gillbeea* are oblong and about 5–8 mm long. The seed coat in the material examined is rather homogeneous in construction, with three or four layers of relatively thick-walled, pigmented, greatly compressed cells. I have not been able to detect a sclerenchymatous layer. The testal epidermis is conspicuously papillate or tuberculate (FIGURE 16). As in other Cunoniaceae, the projections represent unicellular extensions of epidermal cells (FIGURE 17). As observed from sectioned specimens, the tuberculae are broad at the base, with rounded apices and with surface striae extending parallel to the long axis of the projection. Presumably, some of the projections are glandular and secrete the dark, resinous substances that cover the seeds of species of this genus. I have not been able to detect whether the single vascular bundle present at midlength in the seed undergoes subsequent branching.

The fruit of the monotypic South African genus *Platylophus* is derived from a bicarpellate gynoecium and, at maturity, is bilocular but most commonly

one seeded. Its basal region is turgid, and the apical half is distinctly compressed (FIGURE 9). The fruit has been described as an imperfectly dehiscent capsule (Harvey, 1894) that remains closed for an extended period. I have seen no dehiscent fruits.

In *Platylophus* the pericarp is covered by epidermal cells with decidedly thickened and pitted outer and anticlinal walls. A narrow mesocarp is constructed of very thin-walled parenchyma cells, although its veins are surrounded by sclerenchymatous sheathing. A thin, two- or three-layered, fibrous, lignified endocarp is separated from the outer mesocarp by a region containing angular crystals (FIGURE 18).

Seeds are elliptic, less than 1 mm in length, and sometimes with vestigial wings (FIGURE 127). The seed surface is finely reticulate, with the individual cells generally square or rectangular in outline and having slightly raised lateral walls (FIGURE 128). The minute, spherical warts that cover the external cell walls in FIGURE 128 are apparently artifacts, since they were not present in all specimens examined.

The narrow seed coat is relatively undifferentiated and lacks a distinct sclerenchyma layer. Internal to the pigmented outer epidermis is a hypodermis containing scattered angular crystals and two layers of compressed cells that are rectangular in transectional outline. The internal epidermis is similar to the outer one, except that the cells are smaller.

## DISCUSSION

### GENERAL SUMMARY OF FRUIT AND SEED STRUCTURE

Plants belonging to the Cunoniaceae are readily divisible into genera with dehiscent fruits (either follicles or bilocular capsules) and indehiscent ones (dry—capsular or winged; or fleshy—drupes or berries). Fruit wings of *Ceratopetalum* are derived from an expanded and hardened calyx, whereas the winglike outgrowths of *Gillbeea* fruits represent extensions of the gynoecial wall. Dehiscent capsules open septicidally from the apex downward or, less commonly, from the base upward. Fruits of *Ceratopetalum*, *Codia*, and *Pullea* are typically derived from inferior or half-inferior ovaries. Fruit walls range from glabrous to densely pubescent.

Most species of Cunoniaceae produce fruits in which the pericarp becomes differentiated into an exocarp, a mesocarp, and a lignified, fibrous endocarp. The endocarp portion ranges in thickness from about 50  $\mu\text{m}$  in fruits of some species of *Weinmannia* to just over 600  $\mu\text{m}$  in plants of *Geissois*, with a distinct woody endocarp entirely absent only in *Codia* and the fleshy-fruited genus *Anodopetalum*. *Codia* is unique in having aerenchymatous inner pericarp tissue (FIGURES 144, 145). The drupaceous fruits of *Aistopetalum* and (particularly) *Schizomeria* contain an extensive fleshy mesocarp. Fruit walls range in thickness from rather thin (four to eight cells) to very thick (forty cells); they typically contain scattered prismatic or druse crystals, or crystals (rarely acicular ones—*Anodopetalum*) restricted to the inner mesocarp and endocarp. In certain species of *Anodopetalum*, *Ceratopetalum*, *Cunonia*, *Pullea*, and *Schizomeria*, brachysclereids are distributed throughout all three regions of the pericarp.

Dehiscent-fruited genera form one to numerous viable seeds per locule, ranging in length from small (0.4 mm) to rather large (6 mm), with the ovular integuments uniformly developing wings or hairs at maturity. Seeds are generally apically comate, although less commonly hairs are distributed in other patterns. The only exception to the above generalization is the monotypic Australian genus *Acrophyllum*, which forms small, conspicuously papillate (tuberculate) seeds. External seed surfaces are quite diverse in ornamentation. Variable features include shape and wall characteristics of the epidermal cells, and occurrence, type, and abundance of striations and warts.

Seed coats are derived from both ovular integuments and are thin—one to five cells thick, except in *Geissois*, where they may be up to seven cells in thickness. Testae are relatively undifferentiated and generally contain an outer and an inner tanniferous layer. All taxa have a single fibrous layer that, as far as can be determined, is always derived from the outer epidermis of the inner integument. A distinct crystalliferous layer is present in the hypodermis in certain species.

Genera with indehiscent fruits produce one to several seeds per fruit and a variety of seed morphologies. Seeds range in size from small (less than 1 mm in length) in *Codia* and *Pullea* to rather large (up to 5–6 mm in length) in *Aistopetalum* and *Schizomeria*. Although seeds of all genera are devoid of external wall appendages in the form of wings or hairs, those of *Pseudoweinmannia* are unique among the Cunoniaceae in having an arillike outgrowth with the general appearance of an elaiosome. Seed surfaces are smooth (*Pseudoweinmannia*), reticulate (*Codia*, *Pullea*), or papillate (*Gillbeea*).

Mature seed coats are thin (three or four cells), and either undifferentiated and lacking a mechanical zone (*Codia*, *Pullea*) or multiple layered and with a well-differentiated fibrous layer (*Schizomeria*, *Pseudoweinmannia*). Multiple-layered seed coats arise by secondary division within the integumentary layers of fertilized ovules. In *Anodopetalum* multiple seed-coat layers appear to be associated with the absence of a mechanical zone, but this observation requires additional documentation. As in seeds from dehiscent-fruited taxa, one or more crystalliferous layers may be present in certain species.

All cunoniaceous seeds are vascularized by a single bundle, which in some fleshy-fruited genera undergoes branching within the chalaza. All Cunoniaceae have straight embryos that at maturity are embedded in an abundant endosperm.

#### EVOLUTIONARY TRENDS IN FRUIT STRUCTURE AND IN SEED STRUCTURE AND DISPERSAL

The diversity encountered among fruits and seeds of the Cunoniaceae clearly represents a range of different levels of evolutionary advancement and dispersal methods. A major trend of specialization occurs toward the indehiscent condition. A summary of fruit types and methods of seed dispersal in the Cunoniaceae is presented in TABLE 2. Although the bilocular, ventrally dehiscent capsule is the most common fruit type in the family, all available evidence indicates that apocarpy—and the resultant follicular fruits, such as those found in *Acsmithia* and *Spiraeanthemum*—is the primitive condition in the family



TABLE 2. Summary of fruit types and methods of seed dispersal in Cunoniaceae.

| GENUS                   | DISTRIBUTION  | HABIT                                 | FRUIT TYPE | AGENT OF DISPERSAL  | ADAPTATION FOR DISPERSAL                  |
|-------------------------|---|---------------------------------------|------------|---------------------|---|
| DEHISCENT FRUITS        |   |                                       |            |                     |   |
| <u>Acrophyllum</u>      | New South Wales   | Subshrubs                             | Capsule    | ?                   | Seeds papillate                           |
| <u>Acsmithia</u>        | Fiji, New Caledonia,<br>Queensland, New Guinea,<br>Moluccas   | Small to medium<br>trees              | Follicle   | Wind                | Seeds winged                              |
| <u>Bauera</u>           | E Australia   | Small shrubs,<br>subshrubs            | Capsule    | ?                   | ?   |
| <u>Caldcluvia</u>       | Chile, New Zealand,<br>Australia, Philippines,<br>Celebes, Moluccas,<br>New Guinea, Solomon Is.<br>Bougainville Is. | Small to large<br>trees               | Capsule    | Wind                | Seeds winged,<br>papillate,<br>hairy      |
| <u>Callicoma</u>        | E Australia   | Small trees,<br>shrubs                | Capsule    | Wind                | Seeds winged,<br>papillate                |
| <u>Cunonia</u>          | New Caledonia,<br>South Africa  | Small to medium<br>trees, shrubs      | Capsule    | Wind                | Seeds winged                              |
| <u>Geissois</u>         | Fiji, New Caledonia   | Small to medium<br>trees              | Capsule    | Wind                | Seeds winged                              |
| <u>Lamanonia</u>        | Brazil, Paraguay  | Trees, shrubs                         | Capsule    | Wind                | Seeds winged                              |
| <u>Pancheria</u>        | New Caledonia   | Small trees,<br>shrubs                | Capsule    | Wind                | Seeds winged                              |
| <u>Spiraeanthemum</u>   | Samoa, Fiji, New Hebrides,<br>Solomon Is., New Britain,<br>Bougainville Is.   | Shrubs, small to<br>medium trees      | Follicle   | Wind                | Seeds winged                              |
| <u>Vesselowskya</u>     | E Australia   | Small trees, shrubs                   | Capsule    | Wind                | Seeds winged                              |
| <u>Weinmannia</u>       | Old and New World<br>tropics  | Small to medium<br>trees, shrubs      | Capsule    | Wind                | Seeds hairy                               |
| INDEHISCENT FRUITS      |   |                                       |            |                     |   |
| <u>Aistopetalum</u>     | New Guinea  | Tall trees                            | Drupe      | Animals(?)          | Fruits fleshy                             |
| <u>Anodopetalum</u>     | Tasmania  | Shrubs                                | Berry      | Animals(?)          | Fruits fleshy                             |
| <u>Ceratopetalum</u>    | E Australia, New Guinea   | Large shrubs, small<br>to large trees | Capsule    | Wind                | Fruits winged                             |
| <u>Codia</u>            | New Caledonia   | Shrubs, small<br>trees                | Capsule    | Wind                | Fruits hairy                              |
| <u>Gillbeea</u>         | Queensland, New Guinea  | Medium to large<br>trees              | Winged     | Wind                | Fruits winged                             |
| <u>Platylophus</u>      | South Africa  | Medium to large<br>trees              | Capsule    | Water               | Fruits turgid                             |
| <u>Pseudoweinmannia</u> | Queensland,<br>New South Wales  | Large trees                           | Capsule    | Wind (and<br>ants?) | Fruits hairy,<br>seeds with<br>elaiosomes |
| <u>Pullea</u>           | Fiji, Queensland,<br>Moluccas, New Guinea   | Small to medium<br>trees              | Capsule    | ?                   | ?   |
| <u>Schizomeria</u>      | E Australia, New Guinea,<br>Solomon Is.   | Medium to large<br>trees              | Drupe      | Animals(?)          | Fruits fleshy                             |

and is not derived as suggested by Cuatrecasas (1970). The initial evolutionary step, therefore, involved the conversion of a cluster of follicles into a septicidally dehiscent capsule.

In all the genera considered to be primitive on the basis of floral morphology and wood anatomy, the seed is thin walled, has a single, lignified, fibrous layer, and acts as the sole dispersal unit. With the notable exception of *Acrophyllum*, all dehiscent-fruited genera produce seeds with structural modifications—either membranous wings or hairs—for dispersal by wind. Appendages have apparently been lost from the seeds of *Acrophyllum*, although the surface cells have prominent papillae or tuberculate outgrowths. In contrast with other taxa, *Acrophyllum* is a small (usually under 1 m tall) shrub or subshrub that has a very restricted distribution in the Blue Mountains of New South Wales, where it grows only on moist ledges in the immediate vicinity of waterfalls.

Subsequent evolutionary advancement has resulted in major shifts in dispersal methods. In the more advanced Cunoniaceae taxa, the entire fruit has become modified for dispersal and protection, and there have been reductions in the number of seeds per fruit. Distinct trends of structural specialization in the fruit have resulted in densely pubescent (*Codia*, *Pseudoweinmannia*) and winged (*Ceratopetalum*, *Gillbeea*) fruit types that are associated with anemochory. Moreover, the two winged types of fruit represent different evolutionary trends since the wings are derived from different sources (in *Ceratopetalum* they derive from an enlarged and hardened calyx, whereas in *Gillbeea* they are gynoecial in origin). In *Anodopetalum*, *Codia*, and *Bauera* a lignified endocarp in the fruit wall has been lost (Prakash & McAlister, 1977). The adaptive significance of pericarp aerenchyma in *Codia* is unclear. *Pseudoweinmannia*, a tall rainforest tree from Queensland and New South Wales, is interesting in that its densely hairy, indehiscent fruits are undoubtedly scattered by wind, but its elaiosomes suggest that a secondary agent (perhaps an ant) may also be involved in dispersal.

Trends have also occurred toward formation of drupaceous and berrylike fruits. Although method(s) of dispersal for these fruit types is unknown for the Cunoniaceae, such adaptations generally promote seed dispersal by animals. For *Platylophus*, which usually grows near streams and rivers, Ridley (1930) repeated earlier observations that the fruits are dispersed by flowing water. Ben-Erik van Wyk, of the University of Stellenbosch, has observed (pers. comm.) that the turgid capsules break off, leaving the entire pedicel on the inflorescence, and that capsules are frequently seen floating on water. The inflated fruit wall and the absence of dispersal structures on the small, thin-walled seeds may be reflections of this adaptation. Within the family there have thus been major adaptive shifts in dispersal agents—from wind to animal, and even water.

Seeds have undergone concomitant changes. Accompanying the general loss of dispersal appendages, at least two distinct trends are evident in seed-coat structure: reduction in seed-coat thickness, including the loss of a mechanical layer (e.g., *Codia*, *Platylophus*, *Pullea*); and amplification of the seed coat by secondary division of integumentary cells in the fertilized ovule to form a

multiple-layered seed coat (e.g., *Aistopetalum*, *Schizomeria*). A secondary increase in seed-coat layers may or may not be accompanied by loss of a fibrous layer. I cannot accept Krach's (1977) suggestion that all seed coats in the Cunoniaceae were derived via a general trend toward reduction from a multilayered ancestral condition. The various genera of Cunoniaceae are, therefore, good examples of what Corner (1958) and later Stebbins (1970, 1974) referred to as the "transference of function" with respect to the protection and dispersal of seeds. I am uncertain of the significance of the resinous coating on seeds of *Gillbeea*.

It is of interest to note the general correlation between the production of indehiscent fruits with more specialized seed types and a more advanced wood anatomy. The genera *Aistopetalum*, *Anodopetalum*, *Bauera*, *Ceratopetalum*, *Codia*, *Pseudoweinmannia*, and *Schizomeria* all have vessel elements with exclusively or predominantly simple perforation plates (Dickison, 1980b). The only exceptions to this correlation are *Gillbeea* and *Pullea*, which have vessel elements with scalariform perforations.

#### FRUIT AND SEED MORPHOLOGY AND INTRA-FAMILIAL SYSTEMATICS

I have previously pointed out (Dickison, 1980b) that evidence is accumulating to indicate that many of the tribes of Cunoniaceae, as defined by Engler (1928), are very unnatural assemblages that should be either reconstructed or abandoned. The morphology of fruits and seeds supports this opinion. Although the family can be divided into groups and subgroups, representing different levels of specialization, by the use of various characters, it is clear that fruit morphology should be important in any future subdivision of the family.

Engler's tribe Belangereae, containing the southwestern Pacific genus *Geissois* and the Neotropical *Lamanonia*, is from all indications a natural grouping. The two genera both lack petals and have numerous stamens and a bicarpellate superior gynoecium that matures into a septicidally dehiscent capsule containing comparatively large winged seeds. Both also have a structurally advanced wood anatomy (Dickison, 1980b) that is correlated with other indices of advancement such as fourth-rank leaves (*sensu* Hickey, 1971) and, at least in *Geissois*, multilacunar nodal anatomy (Dickison, 1980a).

I emphasized in an earlier paper (Dickison, 1980b) that the tribe Spiraeanthemeae is a very heterogeneous aggregation that includes the primitive genus *Spiraeanthemum* (including the segregate genus *Acsmithia*), with primitive wood anatomy, as well as the rather advanced genus *Aistopetalum*. Extreme diversity is also apparent in reproductive morphology. *Spiraeanthemum* (and *Acsmithia*) have follicular fruits with winged seeds, whereas the drupaceous fruit of *Aistopetalum* and the winged fruit of *Gillbeea* are both significantly more advanced and represent quite different dispersal methods. Although all species in this tribe have flowers with a mostly three- to five-carpellate gynoecium and a stamen number equal to or double the number of sepals, they differ with respect to such other characters as sepal aestivation (imbricate or valvate)

and gynoecium type (apocarpous to syncarpous). The genus *Aphanopetalum* appears to be best removed from the family for reasons previously outlined (Dickison, 1980b).

Engler defined his Cunonieae, the largest tribe of Cunoniaceae, by the following characters: stamens equal to or double the number of sepals; gynoecium superior, bicarpellate, with the carpels more or less fused ventrally in the region of the ovary; petals present or absent; sepals imbricate or valvate; and flowers not produced in a dense spherical head.

On the basis of vegetative anatomy, this is the most diverse group, with genera representing quite different levels of evolutionary advancement (Dickison, 1980b). This is also true for the fruits and seeds of the tribe, which represent major differences in dispersal methods. Both dehiscent and indehiscent fruits are present. The most frequent type is the dehiscent capsule, such as occurs in *Acrophyllum*, *Caldcluvia*, *Cunonia*, *Vesselowskyia*, and *Weinmannia*. There are also more advanced, indehiscent capsules (*Ceratopetalum*, *Pseudoweinmannia*), drupes (*Schizomeria*), and berries (*Anodopetalum*).

Hoogland (1979) has reduced the Australasian genera *Ackama* A. Cunn., *Betchea* Schltr. (including *Stollaea* Schltr.), *Opocunonia* Schltr., and *Spiraeopsis* Miq. to synonymy with the monotypic Chilean genus *Caldcluvia*. The diversity in wood structure among these taxa has already been discussed (Dickison, 1980b). Hoogland (1979) noted that the flowers and fruits of these species are too much alike to merit recognition as separate genera. The seeds, however, are different, as was pointed out by Hoogland. The three Australian and New Zealand species formerly included in *Ackama* all have hairy seeds and similar surface patterns, with epidermal cells having conspicuously undulate anticlinal walls. All other taxa in this complex have winged, frequently papillate seeds with striate or nonstriate (*C. nymanii*) epidermal cells.

Hoogland (1979) further stated that *Caldcluvia* is similar to *Weinmannia* in flower and fruit, being most easily separated on the basis of inflorescence structure. In addition, relationship between *Caldcluvia* and *Weinmannia* is indicated by the occurrence of apically comate seeds in species of both genera. It should also be reemphasized that the only apparent characters that would argue against a merger of *Weinmannia* and *Cunonia* are those associated with fruit dehiscence and seed morphology. Seeds of *Weinmannia* are always hirsute, whereas those of *Cunonia* are uniformly winged. Since both character states currently exist in *Caldcluvia*, however, the strength of this distinction is weakened.

In Engler's scheme the tribe Pancherieae, which contains the three genera *Callicoma*, *Codia*, and *Pancheria*, is held together by flowers that are characteristically produced in tightly compacted, globose clusters. Xylem anatomy is quite variable among these genera, which also show both imbricate and valvate sepal aestivation, superior and inferior gynoecia, and dehiscent (*Callicoma*, *Pancheria*) and indehiscent (*Codia*) fruits producing seeds of quite different structure. The fruits of *Codia*, in contrast to those of *Callicoma* and *Pancheria*, lack a lignified endocarp, and its seeds also lack a mechanical layer. I think that a similar inflorescence type has evolved among diverse elements.

The last tribe, Pulleae, contains the single genus *Pullea*, characterized by a

rather primitive wood structure, apetalous flowers, imbricate sepals, and a bicarpellate, "half-inferior" ovary that matures into an indehiscent capsule. Seeds of *Pullea*, *Codia*, and *Platylophus* are similar in size, in lack of a fibrous layer in the seed coat, and in surface patterns.

The systematic position of the Australian and Tasmanian genus *Bauera* Banks has been somewhat unsettled (Dickison, 1975c). Despite my earlier opinion to the contrary (Dickison, 1975c), recent evidence strongly favors a position in the Cunoniaceae (Bensel & Palser, 1975; Prakash & McAlister, 1977). Aspects of vegetative anatomy would place the genus among the more advanced genera within the family (Dickison, 1980b). The fruits of *Bauera* are dehiscent capsules with seeds that develop a multiple-layered tegmen and apparently lack a mechanical layer (Prakash & McAlister, 1977). This is an uncommon combination of features in the Cunoniaceae, occurring elsewhere only in *Anodopetalum*. A secondary increase in seed-coat layers and an absence of a thick-walled lignified cell layer are both, in my opinion, advanced characteristics among cunoniaceous seeds.

The use of scanning electron microscopy has revealed considerable variation in shape, pattern of hair distribution, and surface characteristics of the seeds. This is particularly true in the large and widely distributed genus *Weinmannia*. Although in a few cases features appear to be diagnostic for species, a much greater sample would need to be examined to assess fully the taxonomic usefulness of seed morphology at the subgeneric and specific levels.

#### COMMENTS ON THE RELATIONSHIPS OF CUNONIACEAE TO OTHER FAMILIES

As reviewed by Dickison (1975a, 1980b), the Cunoniaceae have traditionally been placed in a basal position within the large order Rosales, in or near the saxifragaceous complex (Engler, 1928; Schulze-Menz, 1964; Cronquist, 1981). Families that have long been closely allied with the Cunoniaceae include the Saxifragaceae, Eucryphiaceae, Brunelliaceae, and Staphyleaceae. Since the seed structures of this complex are incompletely known, it would be premature to attempt a discussion of relationships based upon this criterion. However, a few observations can be made.

The present study further substantiates the significant differences in seed-coat structure between the Cunoniaceae (including *Bauera*) and the Saxifragaceae that have been summarized by Prakash and McAlister (1977). Seed coats of the Cunoniaceae are uniformly derived from both integuments, whereas those of the Saxifragaceae apparently mature only from the outer integument, with the inner tegmen degenerating. Corner (1976) has indicated that there is a significant evolutionary distinction between families with exotestal seed construction (Saxifragaceae) and those with exotegmic seed construction (Cunoniaceae). The additional important distinctions (relating to aspects of embryology) between these families require documentation.

The small neotropical family Brunelliaceae, characterized by apocarpous, apetalous, diplostemonous flowers, in this respect resembles the cunoniaceous genera *Acsmithia* and *Spiraeanthemum*. Each carpel matures into a follicle in

which the pericarp becomes strongly differentiated into outer parenchymatous exocarp and inner woody endocarp (Eyde, 1970). The asymmetric growth of the ovary that displaces the style to the abaxial side—and the resulting specialized fruit—is constant in all members of the Brunelliaceae and is not matched in any possibly related family (Cuatrecasas, 1970). Seeds of *Brunellia* lack dispersal appendages, and the testa is thick. Wood anatomy of the genus is at a higher evolutionary level than that of the more primitive genera of Cunoniaceae (Dickison, 1980b).

Over the years various individuals (Hallier, 1908; Linden, 1960; Whitmore, 1972; Thorne, 1976) have strongly emphasized affinities between the Staphyleaceae and the Cunoniaceae. Similarity is evidenced in the fibrous exotegmic seeds of the staphyleaceous genera *Huertea* Ruiz & Pavon and *Tapiscia* D. Oliver (Corner, 1976) and the exotegmic seeds of the Cunoniaceae.

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## EXPLANATION OF PLATES

## PLATE I

FIGURES 1–14. Fruit morphology of Cunoniaceae. 1, *Spiraeanthemum macgillivrayi* (Morrison 25.6.1896),  $\times 5.5$ . 2, *Weinmannia blumei* (Dickison 215),  $\times 5$ . 3, *Cunonia macrophylla* (Webster & Hildreth 14493),  $\times 1.5$ . 4, 5, *Pancheria sebertii* (Franc 2109): 4, mature fruit head,  $\times 1.5$ ; 5, individual fruit valve,  $\times 3$ . 6, *Geissois stipularis* (Fiji Herb. 31297),  $\times 1$ . 7, *Acrophyllum australe* (Stauffer et al. 5700),  $\times 3$ . 8, *Schizomeria ilicina* (Brass 12150),  $\times 1$ . 9, *Platylophus trifoliatus* (Bolus 621),  $\times 3$ . 10, *Gillbeea papuana* (Brass 31815),  $\times 1.5$ . 11, *Ceratopetalum succirubrum* (Hartley 10967),  $\times 1.5$ . 12, 13, *Pseudoweinmannia lachnocarpa* (Clemens 43294),  $\times 2.5$ : 12, mature fruit; 13, mature fruit with tomentum partially removed. 14, *Codia nitida* (Dickison 221),  $\times 2.5$ .

## PLATE II

FIGURES 15–22. Fruit anatomy of Cunoniaceae. 15–17, *Gillbeea papuana* (Brass 31815): 15, transverse section of mature fruit; 16, transverse section of mature seed; 17, seed epidermis showing papillae. 18, *Platylophus trifoliatus* (Bolus 621), transverse section of pericarp. 19, *Acsmithia densiflora* (Dickison 220), transverse section of follicle. 20, *Weinmannia racemosa* (cult., E), transverse section of capsule. 21, *Pseudoweinmannia lachnocarpa* (Dickison & Jessup 294), transverse section of fruit showing placental proliferations. 22, *Geissois stipularis* (Fiji Herb. 31297), transverse section of capsule (only major veins illustrated).

## PLATE III

FIGURES 23–30. Seed-coat structure in Cunoniaceae: 23, *Acsmithia densiflora* (Dickison 220); 24, *Caldcluvia nymanii* (Hoogland & Craven 11069); 25, *Cunonia pulchella* (Dickison 218); 26, *Pancheria hirsuta* (Dickison 227); 27, *Ceratopetalum succirubrum* (Croft & Marsh, LAE 71177); 28, *Vesselowskya rubifolia* (Schodde 3210); 29, *Codia nitida* (Dickison 221); 30, *Acrophyllum australe* (Stauffer et al. 5700) (CR, crystalliferous layer; CU, cuticle; EN, endosperm; EP, epidermis; IT, inner tegmen; S, sclerenchymatous layer; stippled cells pigmented).

## PLATE IV

FIGURES 31–39. Scanning electron micrographs of seeds of Cunoniaceae. 31, 32, *Pancheria confusa* (Veillon 66): 31, side view,  $\times 9$ ; 32, hilar region,  $\times 20$ . 33, 34, *P. sebertii* (Franc 2109): 33, side view,  $\times 9$ ; 34, surface,  $\times 40$ . 35, 36, *P. elegans* (Dickison 158): 35, oblique side view,  $\times 25$ ; 36, surface,  $\times 50$ . 37, 38, *Geissois stipularis* (Fiji Herb. 31297): 37, side view,  $\times 8$ ; 38, surface,  $\times 22$ . 39, *Lamanonia ternata* (Irwin et al. 8603), side view,  $\times 6.5$ .

## PLATE V

FIGURES 40–48. Scanning electron micrographs of seeds of Cunoniaceae. 40, *Lamanonia tomentosa* (Balansa 4752), surface,  $\times 50$ . 41, 42, *Geissois benthamiana* (Forest Guard, Lismore 3.1909), surface: 41,  $\times 50$ ; 42,  $\times 500$ . 43, *G. biagiana* (Dockrill 34), surface,  $\times 500$ . 44, 45, *Cunonia purpurea* (Dickison 144): 44, side view,  $\times 15$ ; 45, surface,  $\times 150$ . 46–48, *C. macrophylla* (Bernardi 9507): 46, oblique side view,  $\times 16$ ; 47, surface,  $\times 50$ ; 48, surface,  $\times 500$ .



## PLATE VI

FIGURES 49–57. Scanning electron micrographs of seeds of Cunoniaceae. 49, 50, *Cunonia schinziana* (McKee 23112): 49, side view,  $\times 14$ ; 50, surface,  $\times 40$ . 51, *C. pseudoverticillata* (McKee 4410), side view,  $\times 20$ . 52, 53, *Spiraeanthemum katakata* (Smith 4371): 52, side view,  $\times 15$ ; 53, surface,  $\times 200$ . 54, *Acsmithia elliptica* (Veillon 2844), side view,  $\times 20$ . 55, 56, *A. densiflora* (Musselman et al. 5222): 55, side view,  $\times 21$ ; 56, surface,  $\times 200$ . 57, *A. reticulata* (Galore & Wood, NGF 41005), side view,  $\times 20$ .

## PLATE VII

FIGURES 58–66. Scanning electron micrographs of seeds of Cunoniaceae, *Caldcluvia*. 58–60, *C. celebica* (Havel & Kairo, NGF 17084): 58, side view,  $\times 30$ ; 59, surface,  $\times 100$ ; 60, papillae,  $\times 300$ . 61, *C. australiensis* (Hoogland 8538), side view,  $\times 20$ . 62, 63, *C. rosifolia* (Walker s.n.): 62, side view,  $\times 50$ ; 63, surface,  $\times 100$ . 64, *C. paniculata* (Dombey 713), surface,  $\times 50$ . 65, *C. brassii* (Brass 29616), side view,  $\times 23$ . 66, *C. clemensiae* (Van Balgooy 969), surface,  $\times 50$ .

## PLATE VIII

FIGURES 67–75. Scanning electron micrographs of seeds of Cunoniaceae, *Caldcluvia*. 67, 68, *C. paniculosa* (Thorne et al. 25938): 67, side view,  $\times 20$ ; 68, surface,  $\times 200$ . 69, 70, *C. papuana* (Kalkman 5316): 69, side view,  $\times 50$ ; 70, surface,  $\times 500$ . 71, 72, *C. fulva* (Van Royen, NGF 18266): 71, oblique side view,  $\times 30$ ; 72, surface,  $\times 500$ . 73–75, *C. nymanii* (Stevens, NGF 50443): 73, side view,  $\times 15$ ; 74, surface,  $\times 50$ ; 75, surface,  $\times 500$ .

## PLATE IX

FIGURES 76–84. Scanning electron micrographs of seeds of Cunoniaceae. 76–78, *Callicoma serratifolia* (White 10279): 76, oblique side view,  $\times 30$ ; 77, surface,  $\times 200$ ; 78, detail of papillae,  $\times 100$ . 79, 80, *Acrophyllum australe* (Stauffer et al. 5700): 79, side view,  $\times 50$ ; 80, detail of surface,  $\times 500$ . 81, 82, *Vesselowskya rubifolia* (White 11482): 81, side view,  $\times 15$ ; 82, surface,  $\times 150$ . 83, 84, *Weinmannia tannaensis* (Bernardi 12909): 83, side view,  $\times 30$ ; 84, surface,  $\times 300$ .

## PLATE X

FIGURES 85–93. Scanning electron micrographs of seeds of Cunoniaceae, *Weinmannia*. 85, 86, *W. racemosa* (Philipson et al. 349): 85, oblique side view,  $\times 14$ ; 86, surface,  $\times 100$ . 87, *W. subsessiliflora* (Vasquez A130), side view,  $\times 23$ . 88, 89, *W. monticola* (McKee 23892): 88, side view,  $\times 40$ ; 89, surface,  $\times 400$ . 90, *W. pinnata* (Sousa & Rico 8118), side view,  $\times 24$ . 91, *W. tinctoria* (Bernardi 14516), oblique side view (arrow points to hilum),  $\times 20$ . 92, 93, *W. pullei* (Hoogland & Schodde 7242): 92, side view,  $\times 16$ ; 93, surface,  $\times 350$ .

## PLATE XI

FIGURES 94–102. Scanning electron micrographs of seeds of Cunoniaceae, *Weinmannia*. 94, 95, *W. richii* (A. C. Smith 6813): 94, side view,  $\times 40$ ; 95, surface,  $\times 200$ . 96, *W. rubrinervis* (D'Alleizette s.n.), side view,  $\times 20$ . 97, 98, *W. serrata* (Bernardi 12816): 97, side view,  $\times 40$ ; 98, surface,  $\times 1000$ . 99, *W. sylvicola* (Van Steenis 22314), surface,  $\times 500$ . 100, 101, *W. luzoniensis* (Gacad, FB 27274): 100, side view,  $\times 40$ ; 101, surface,  $\times 500$ . 102, *W. glabra* (Lansberger s.n.), side view,  $\times 50$ .

## PLATE XII

FIGURES 103–111. Scanning electron micrographs of seeds of Cunoniaceae, *Weinmannia*. 103, 104, *W. negrosensis* (Ramos, *Philippine Plants* 1287): 103, oblique side view,  $\times 20$ ; 104, surface,  $\times 1000$ . 105, *W. mauritiana* (D'Alleizette 2166), side view,  $\times 40$ . 106, 107, *W. descombesiana* (Eyma 3590): 106, side view,  $\times 40$ ; 107, surface,  $\times 200$ . 108, *W. trichophora* (Pullen 374), side view,  $\times 20$ . 109–111, *W. fraxinea* (Foreman 51): 109, oblique side view,  $\times 20$ ; 110, surface,  $\times 200$ ; 111, surface,  $\times 500$ .

## PLATE XIII

FIGURES 112–120. Scanning electron micrographs of seeds of Cunoniaceae, *Weinmannia*. 112, 113, *W. trichosperma* (Zollner 3137): 112, side view,  $\times 40$ ; 113, surface,  $\times 500$ . 114, *W. vescoi* (Van Balgooy 1796), surface,  $\times 200$ . 115, 116, *W. celebica* (Van Balgooy 3809): 115, side view,  $\times 40$ ; 116, surface,  $\times 200$ . 117, *W. hutchinsonii* (Mendoza, *PNH* 18409), surface,  $\times 200$ . 118, *W. purpurea* (Kajewski 1738), surface,  $\times 400$ . 119, *W. denhamii* (Bernardi 13258), surface,  $\times 200$ . 120, *W. decora* (Bernardi 11961), surface,  $\times 300$ .

## PLATE XIV

FIGURES 121–129. Scanning electron micrographs of seeds of Cunoniaceae. 121, 122, *Codia nitida* (Jaffre 2223): 121, side view,  $\times 60$ ; 122, surface,  $\times 200$ . 123, *Pullea stutzeri* (Irvine 1253), side view,  $\times 100$ . 124, *P. glabra* (Brass 31156), side view,  $\times 100$ . 125, 126, *Pseudoweinmannia lachnocarpa* (Clemens 43294): 125, side view (arrows point to arillike outgrowth),  $\times 2$ ; 126, detail of outgrowth,  $\times 75$ . 127, 128, *Platylophus trifolius* (Bolus 621): 127, side view,  $\times 50$ ; 128, surface,  $\times 500$ . 129, *Schizomeria whitei* (Dickison 205), surface,  $\times 2000$ .

## PLATE XV

FIGURES 130–136. Structure of fruits and seeds in Cunoniaceae, transverse sections. 130, 131, *Cunonia balansae* (Dickison 230): 130, immature fruit; 131, young seed. 132, 133, *C. pterophylla* (Dickison 238): 132, immature fruit; 133, seed. 134, *Pancheria robusta* (Dickison 248), young seed. 135, *Caldcluvia nymanii* (Hoogland & Craven 11069), mature seed. 136, *Acsmithia densiflora* (Dickison 220), seed coat. (C, cotyledon; EN, endosperm; EP, epidermis; IT, inner tegmen; P, papillae; S, sclerenchymatous layer; VB, vascular bundle.)

## PLATE XVI

FIGURES 137–145. Structure of fruits and seeds in Cunoniaceae. 137–140, *Aistopetalum multiflorum* (Hoogland & Craven 10826): 137, immature fruit, transverse section; 138, immature fruit, longitudinal section; 139, hilar end of young seed, transverse section; 140, chalazal end of young seed, transverse section. 141, 142, *Schizomeria ovata* (Hoogland 11684), transverse sections: 141, young seed; 142, outer portion of seed coat. 143, *Anodopetalum biglandulosum* (Webb 3337), inner region of pericarp, transverse section. 144, 145, *Codia nitida* (Dickison 221), transverse sections: 144, fruit; 145, pericarp. (CR, crystalliferous layer; E, endocarp; EP, epidermis; IT, inner tegmen; S, sclerenchymatous layer; VB, vascular bundle.)

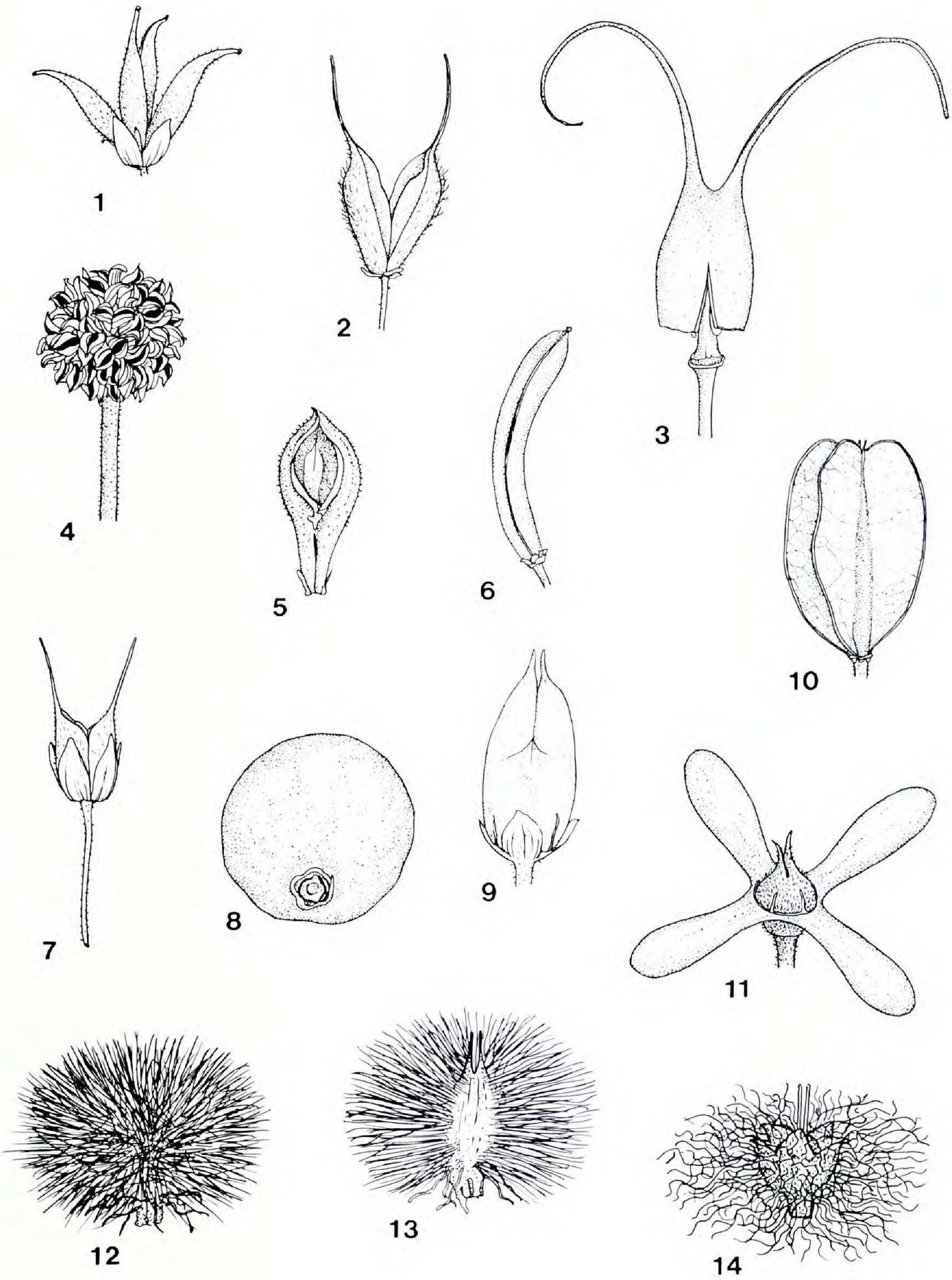


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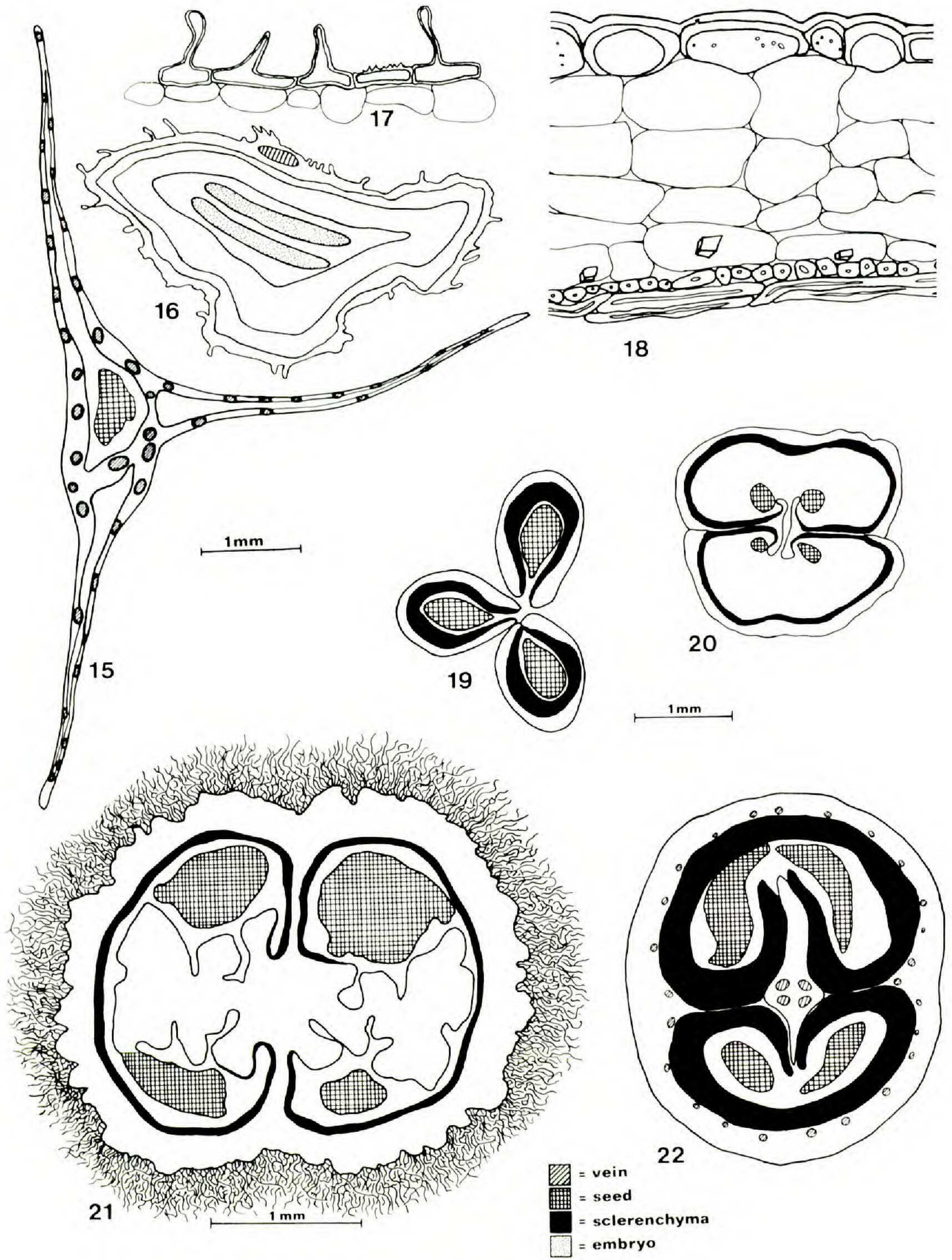
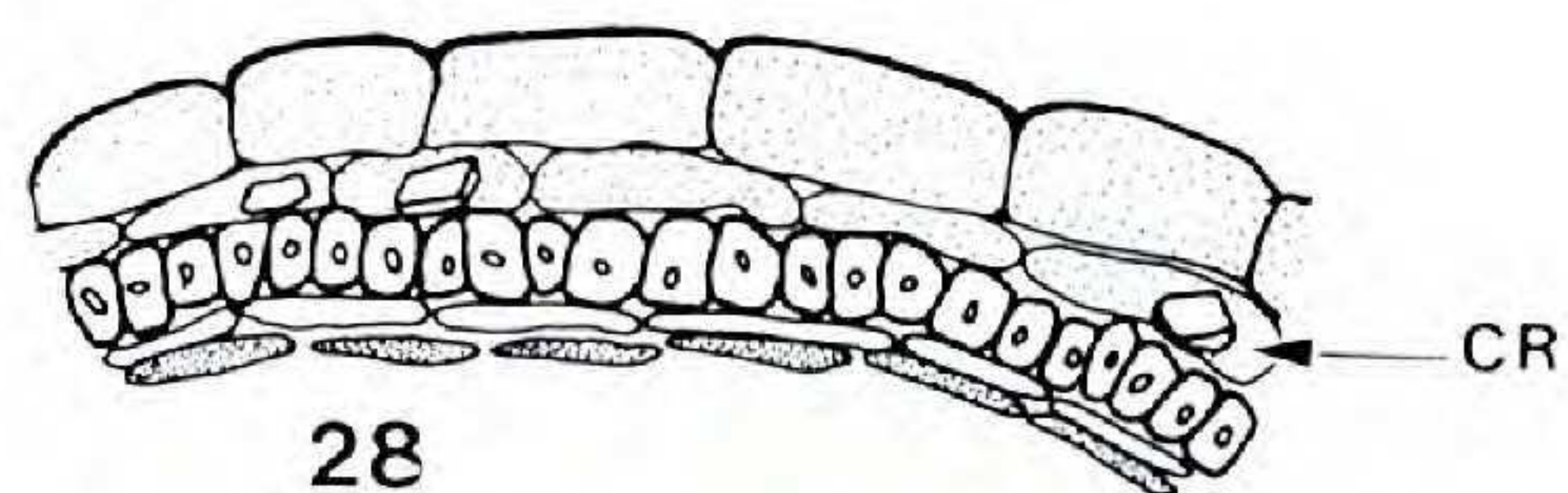
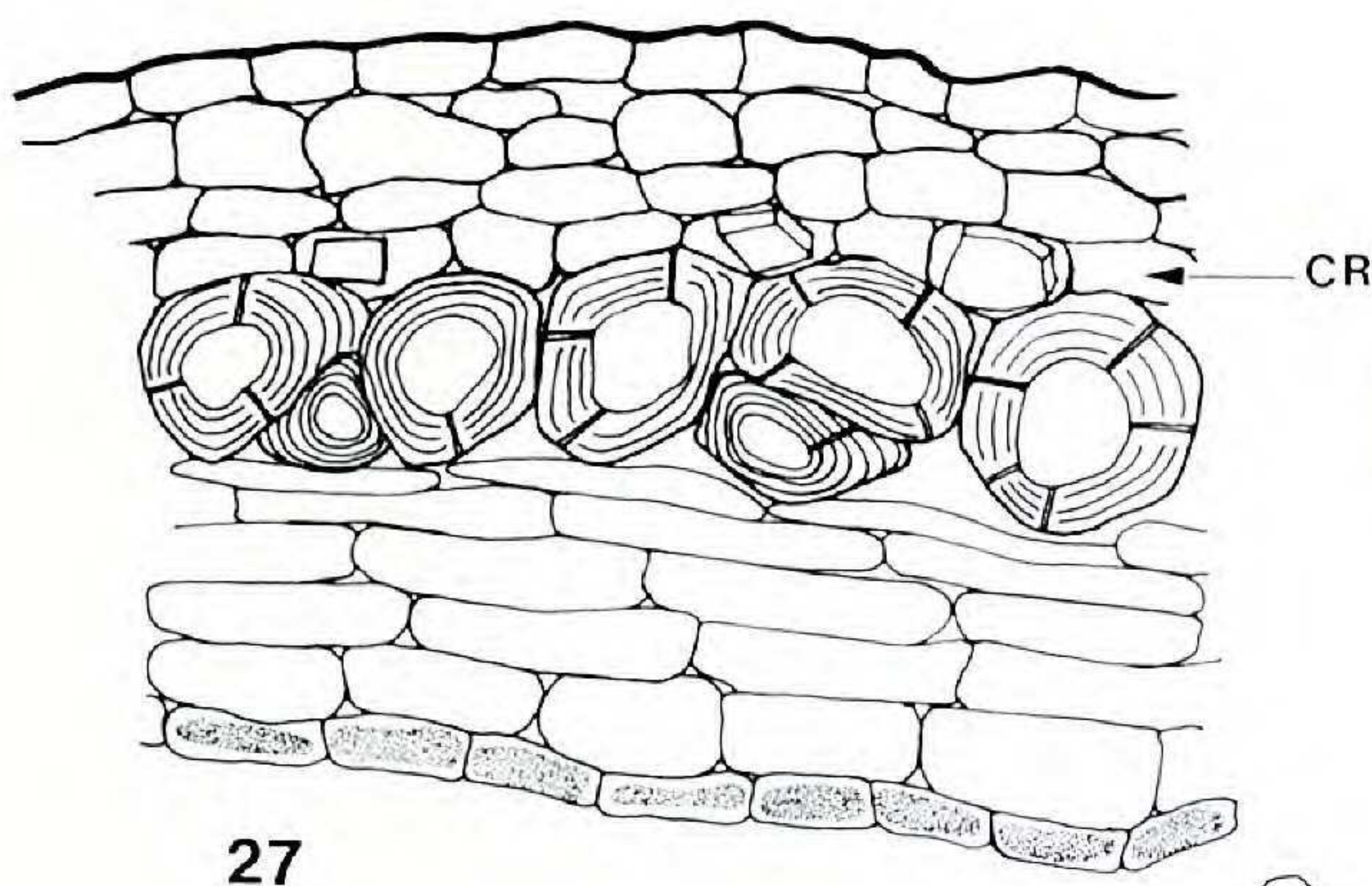
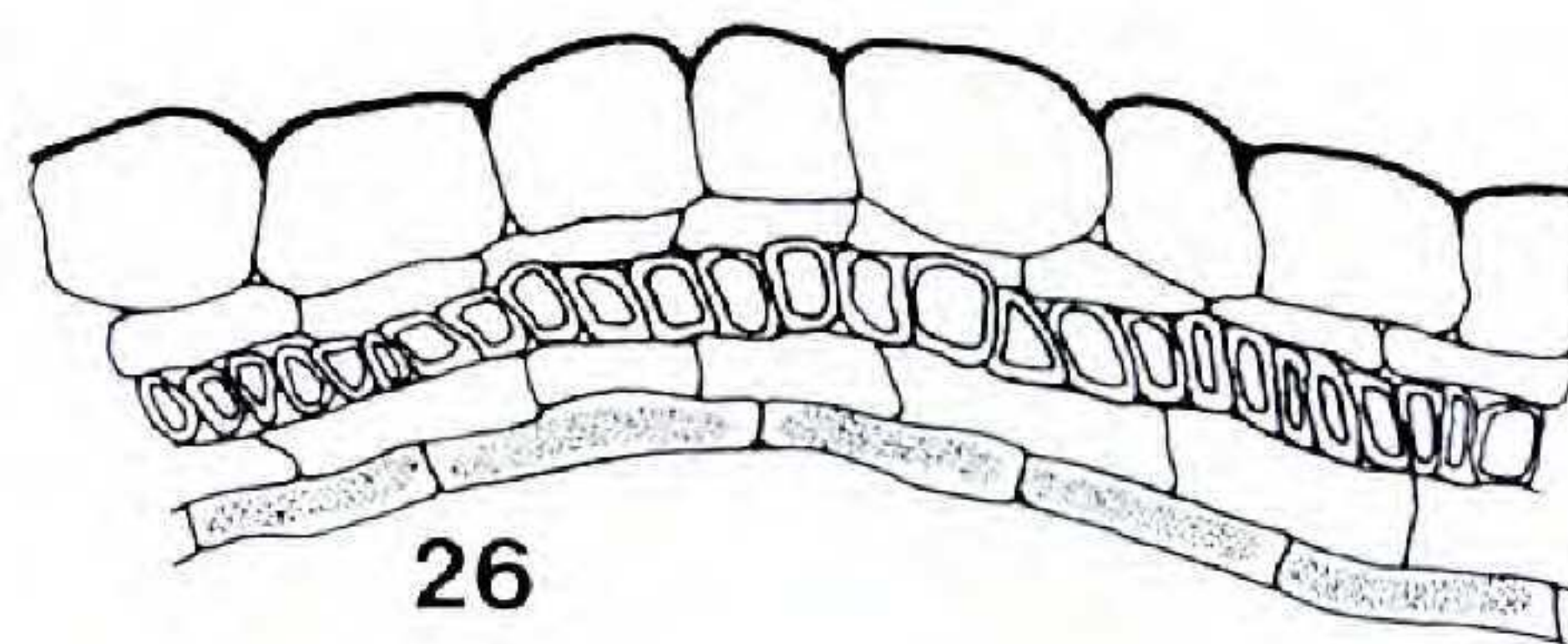
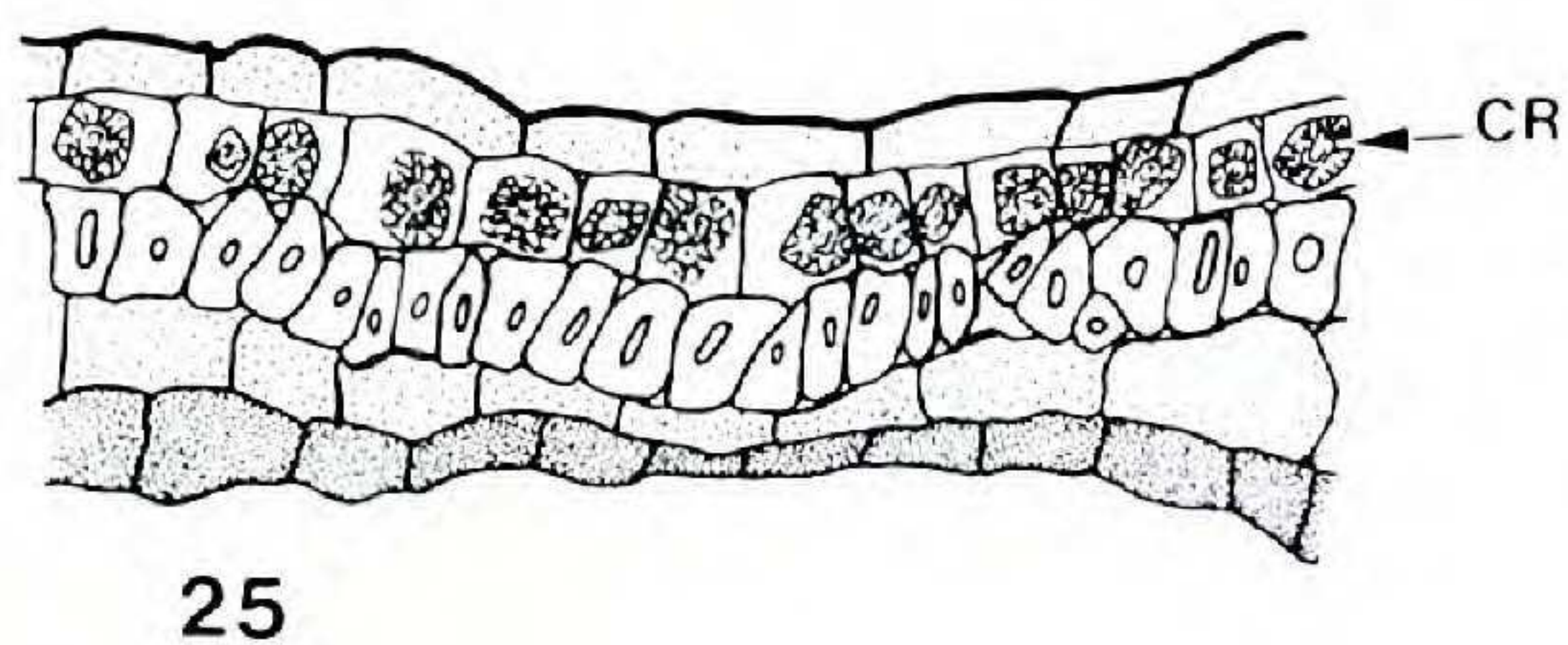
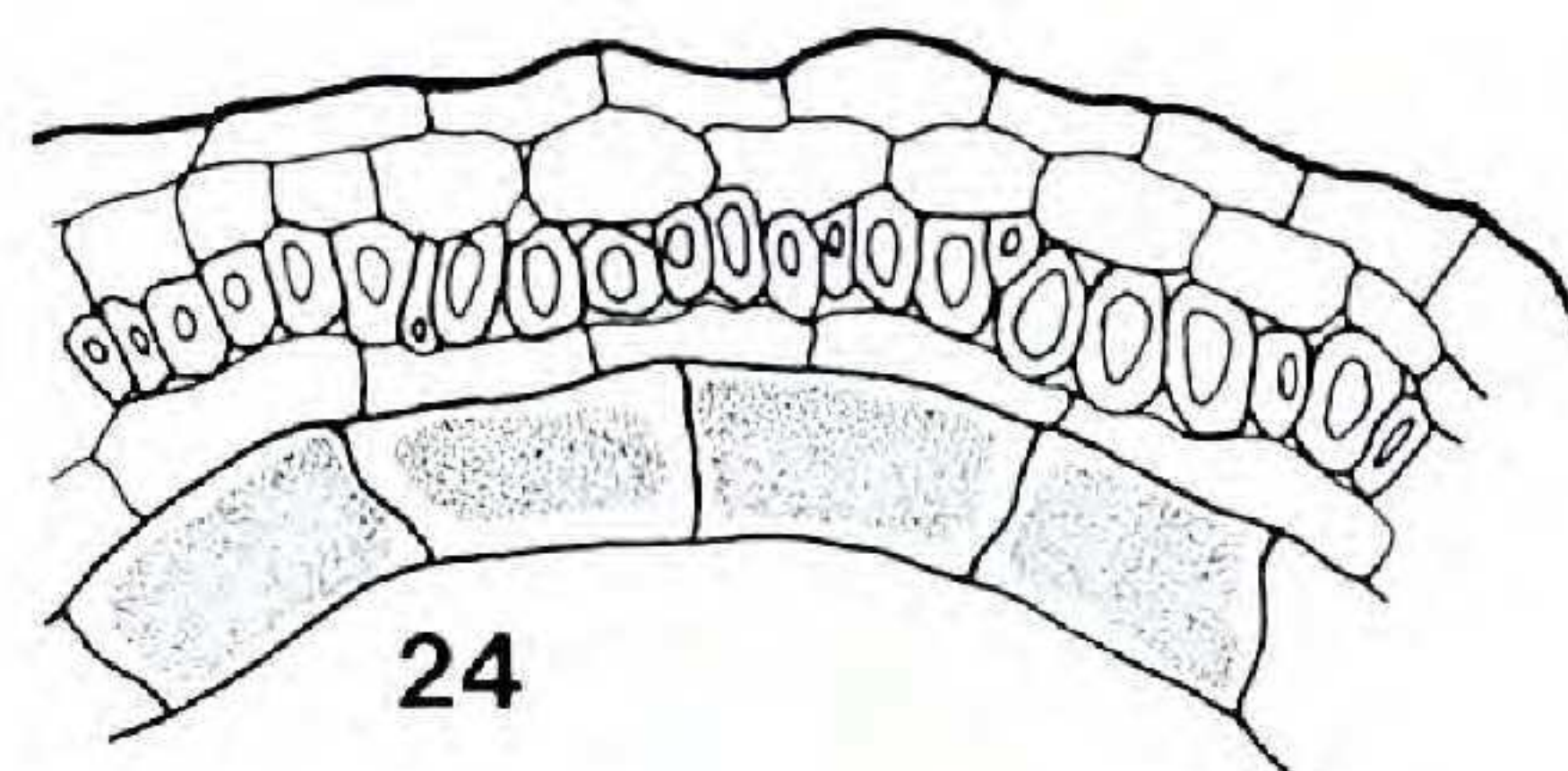
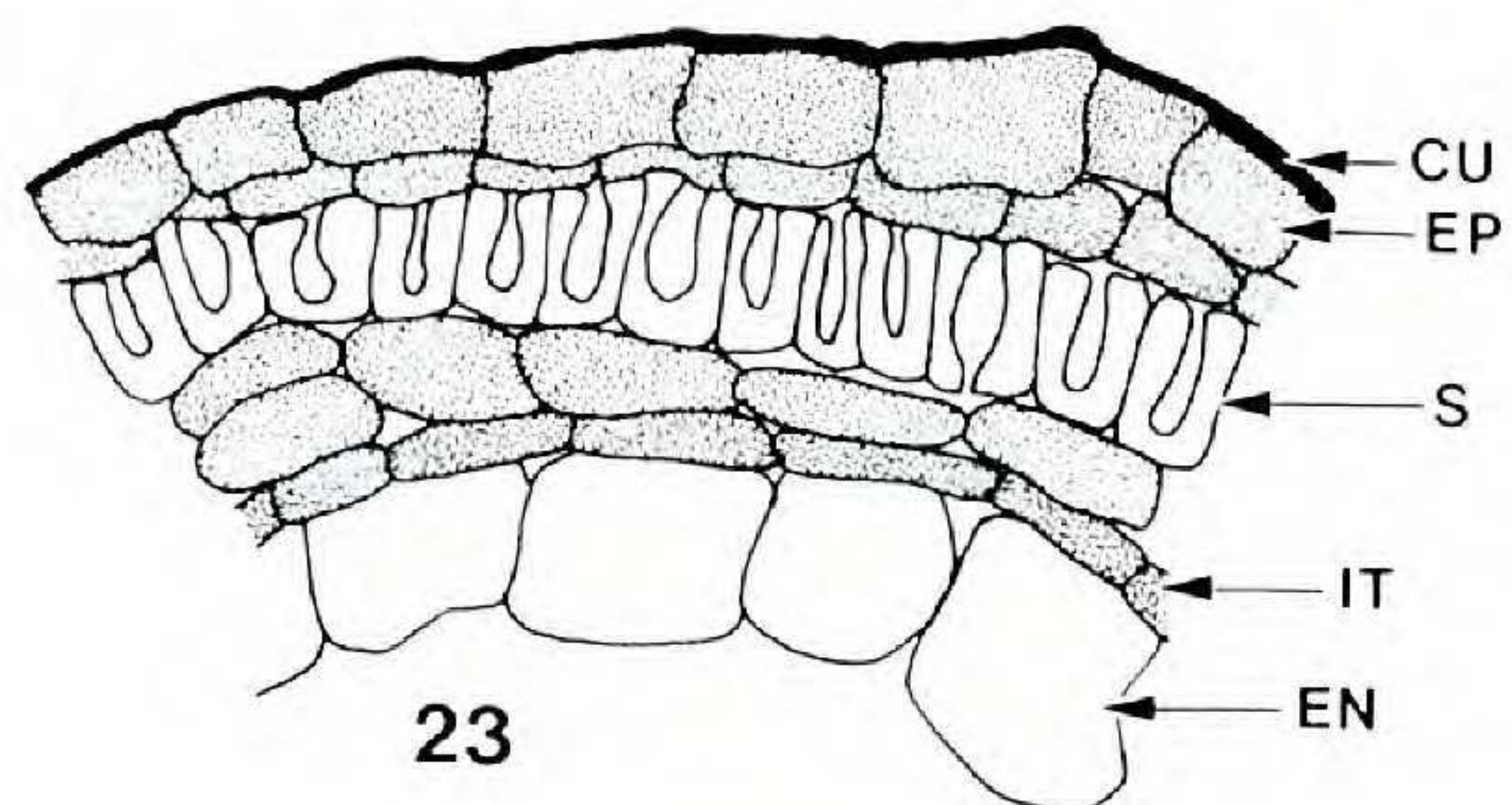


PLATE II



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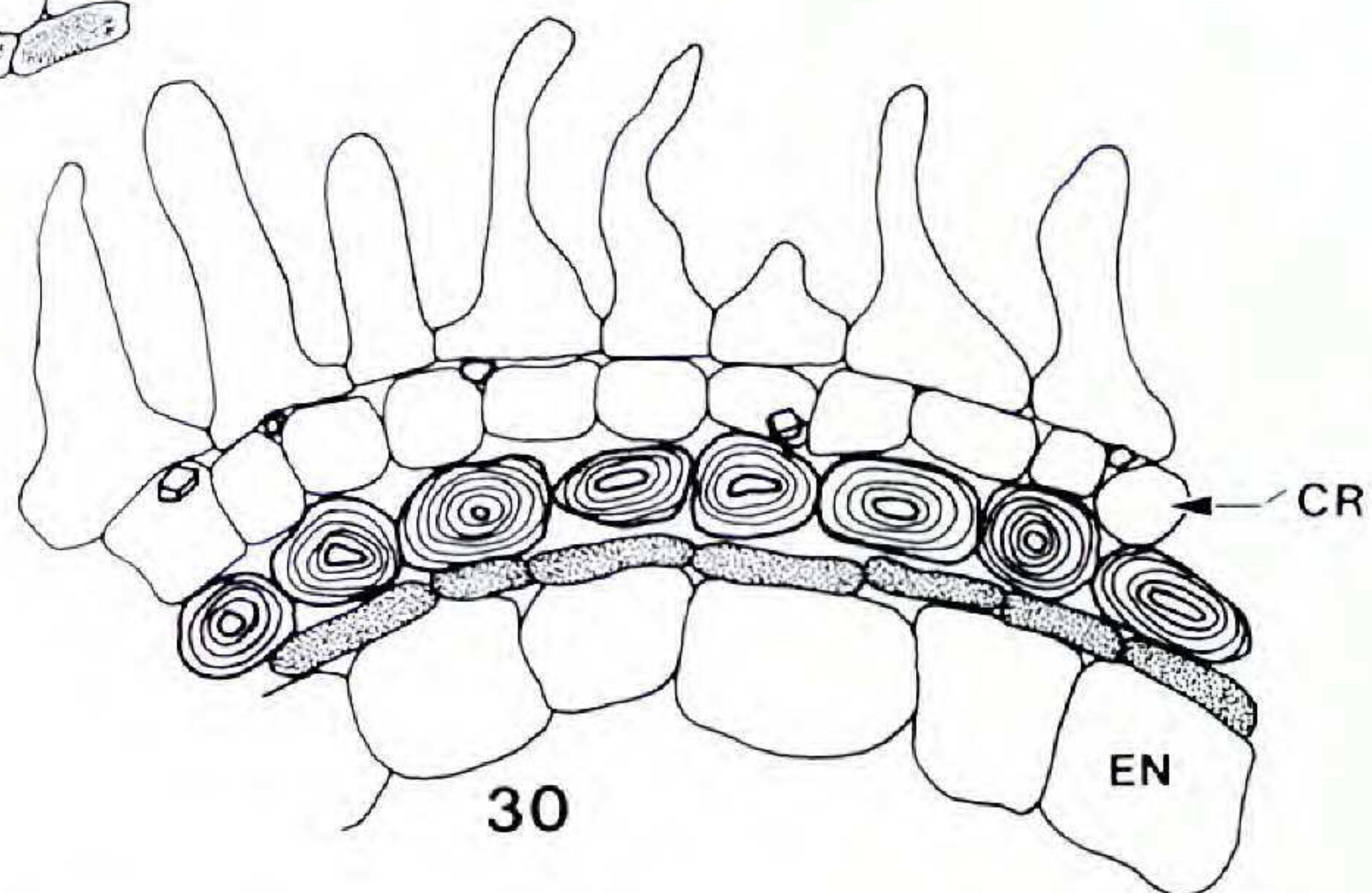
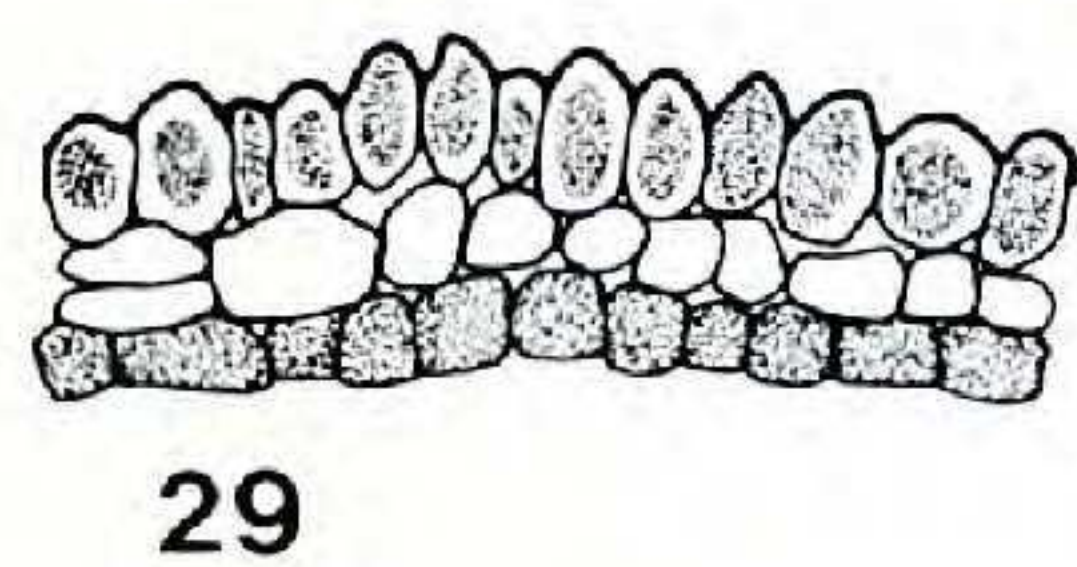


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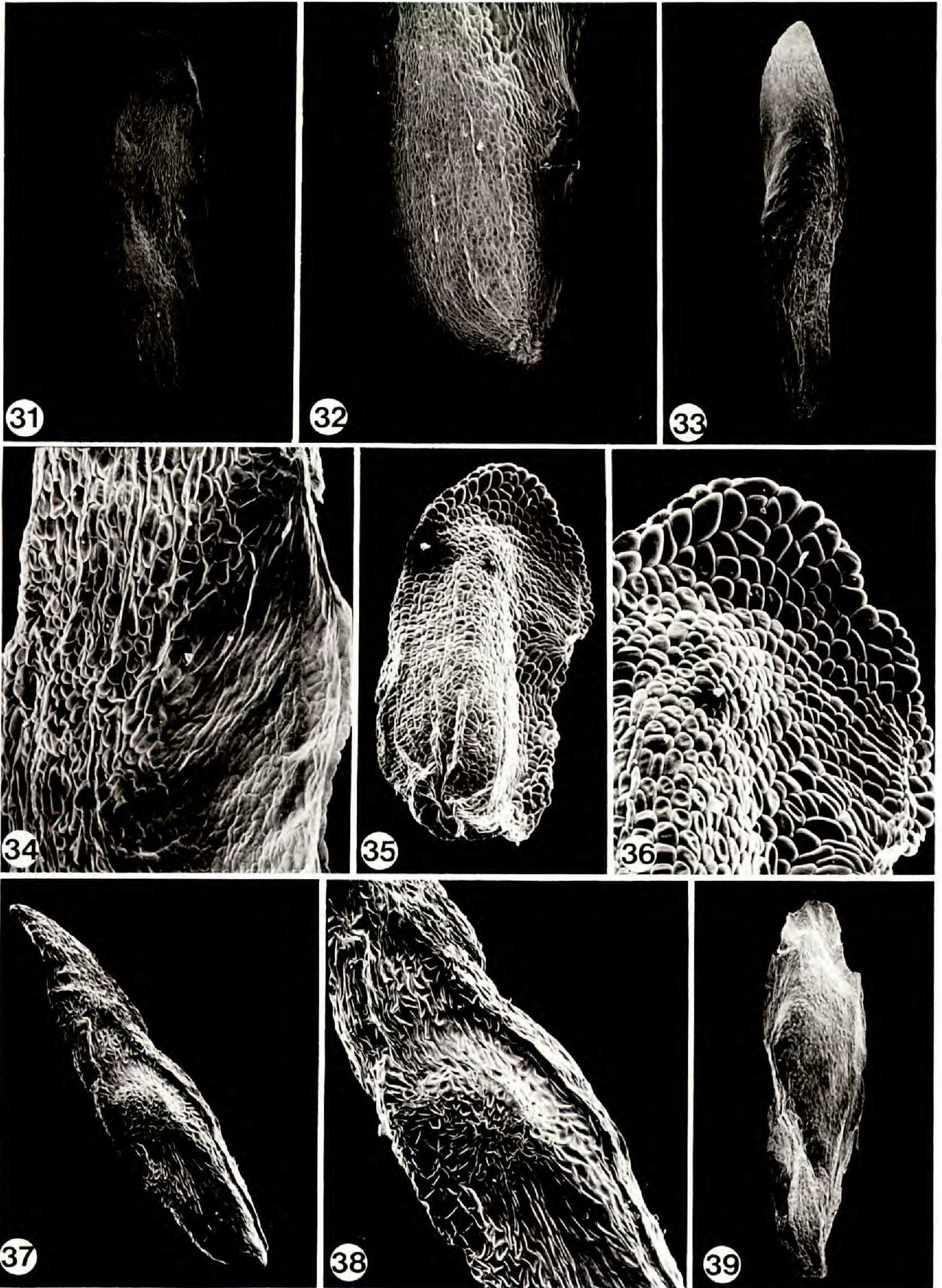


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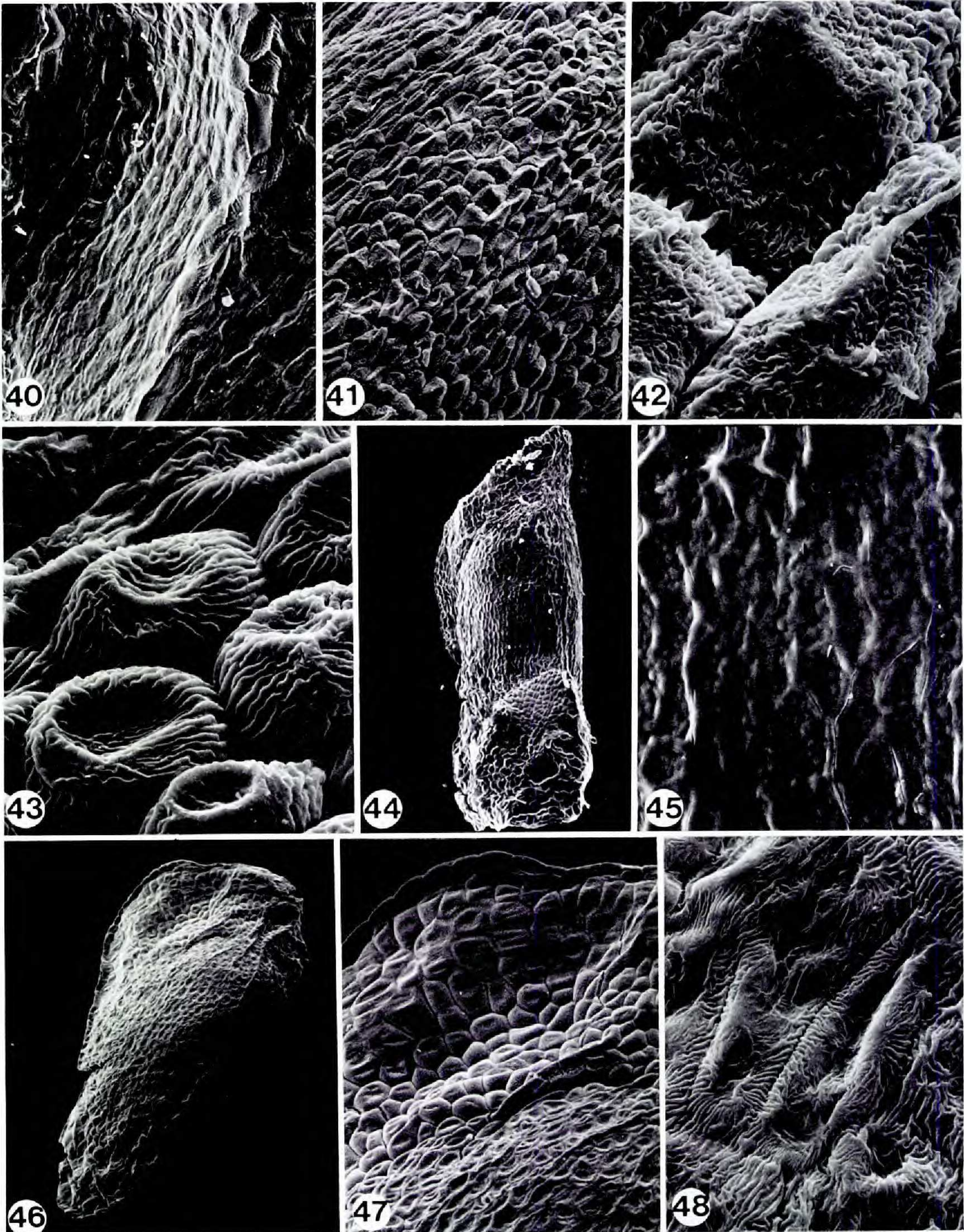


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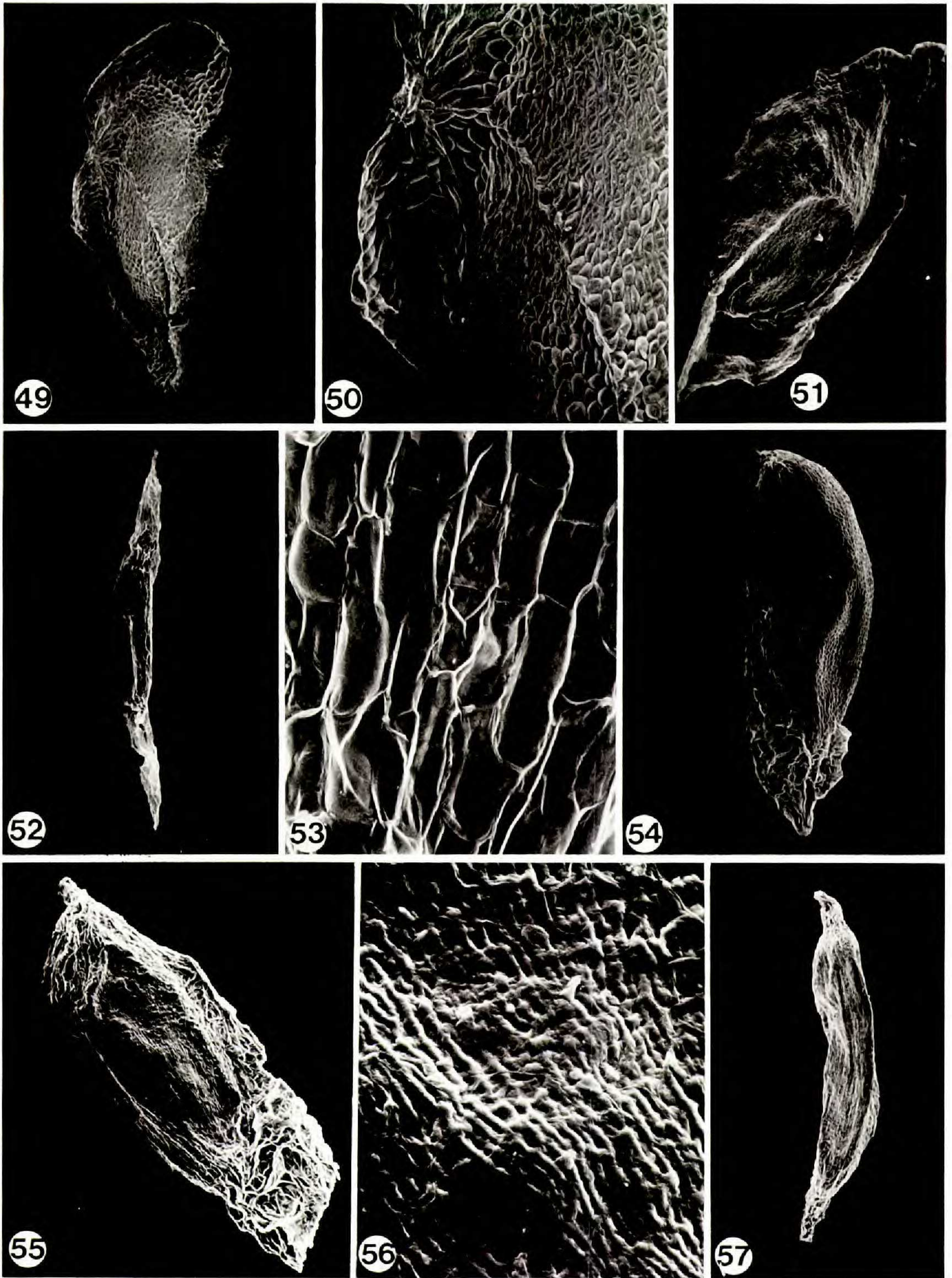


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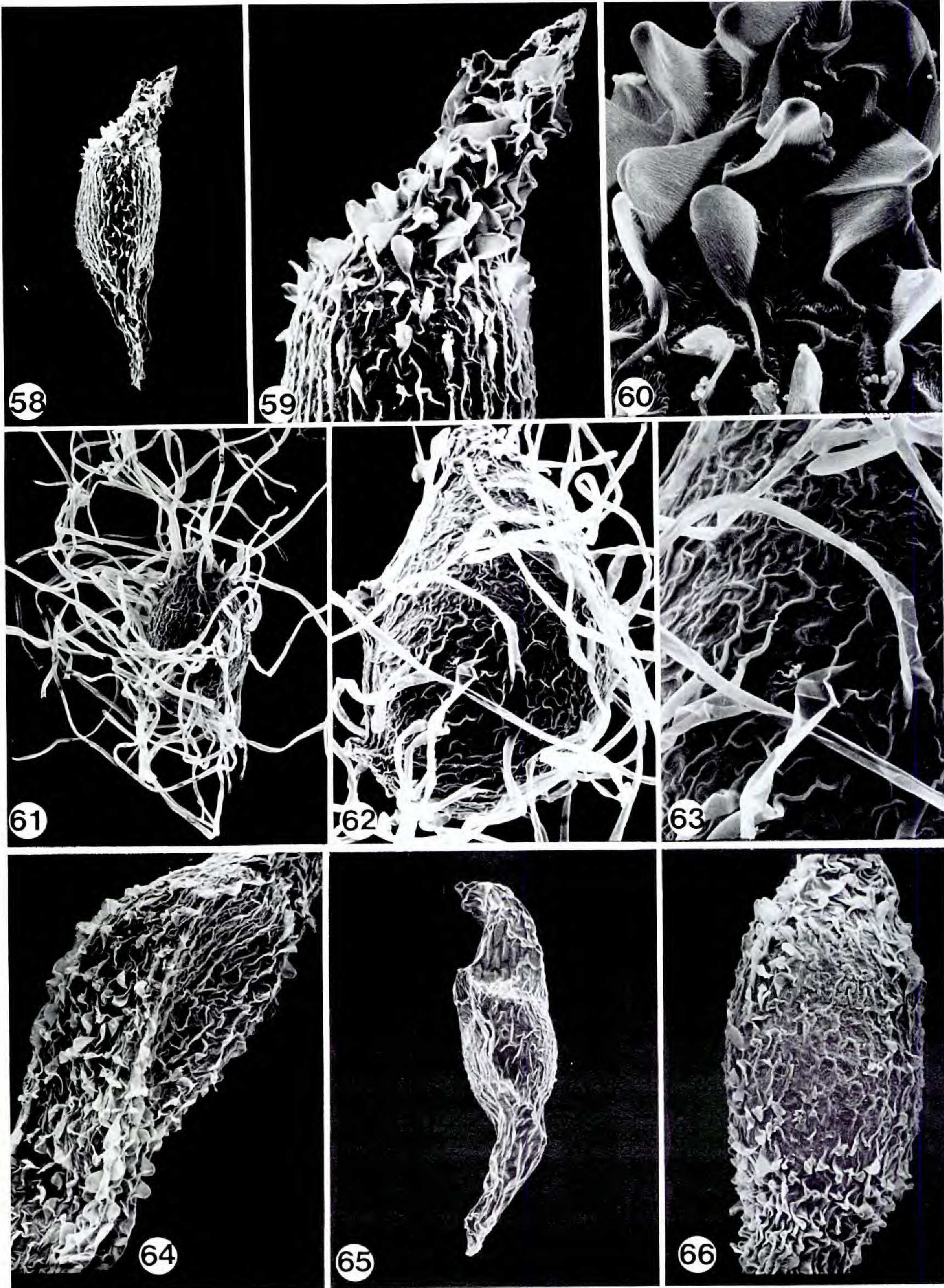


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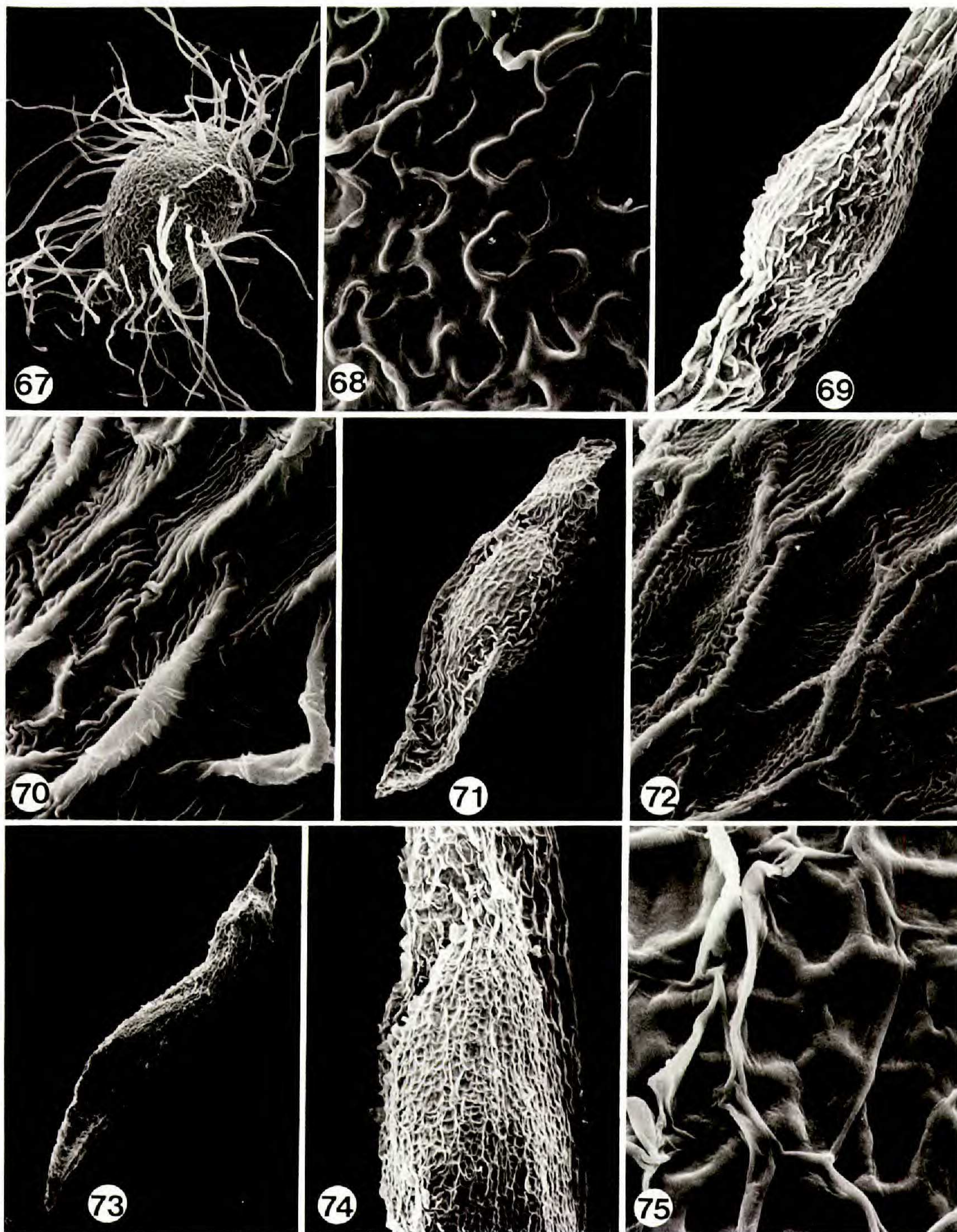


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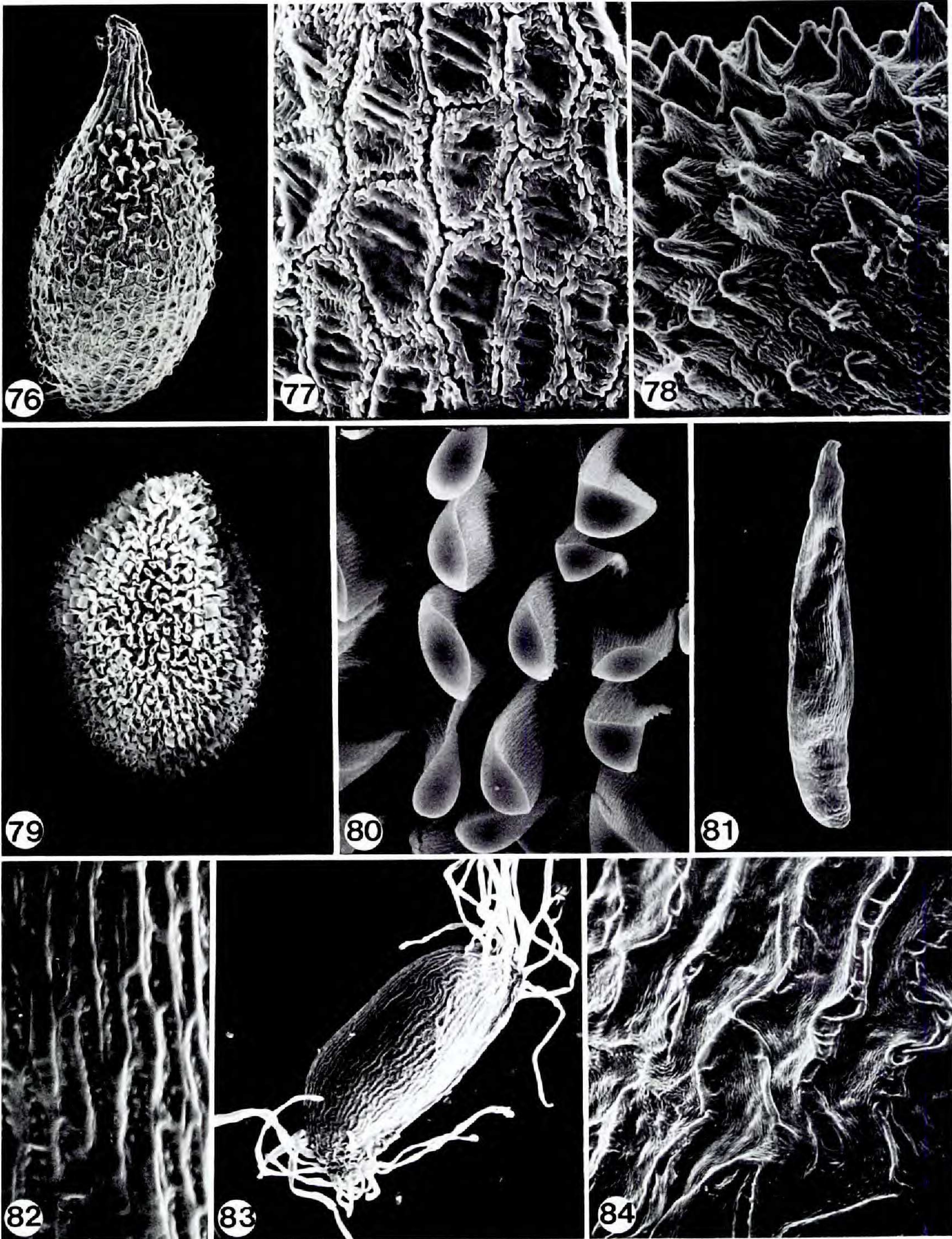


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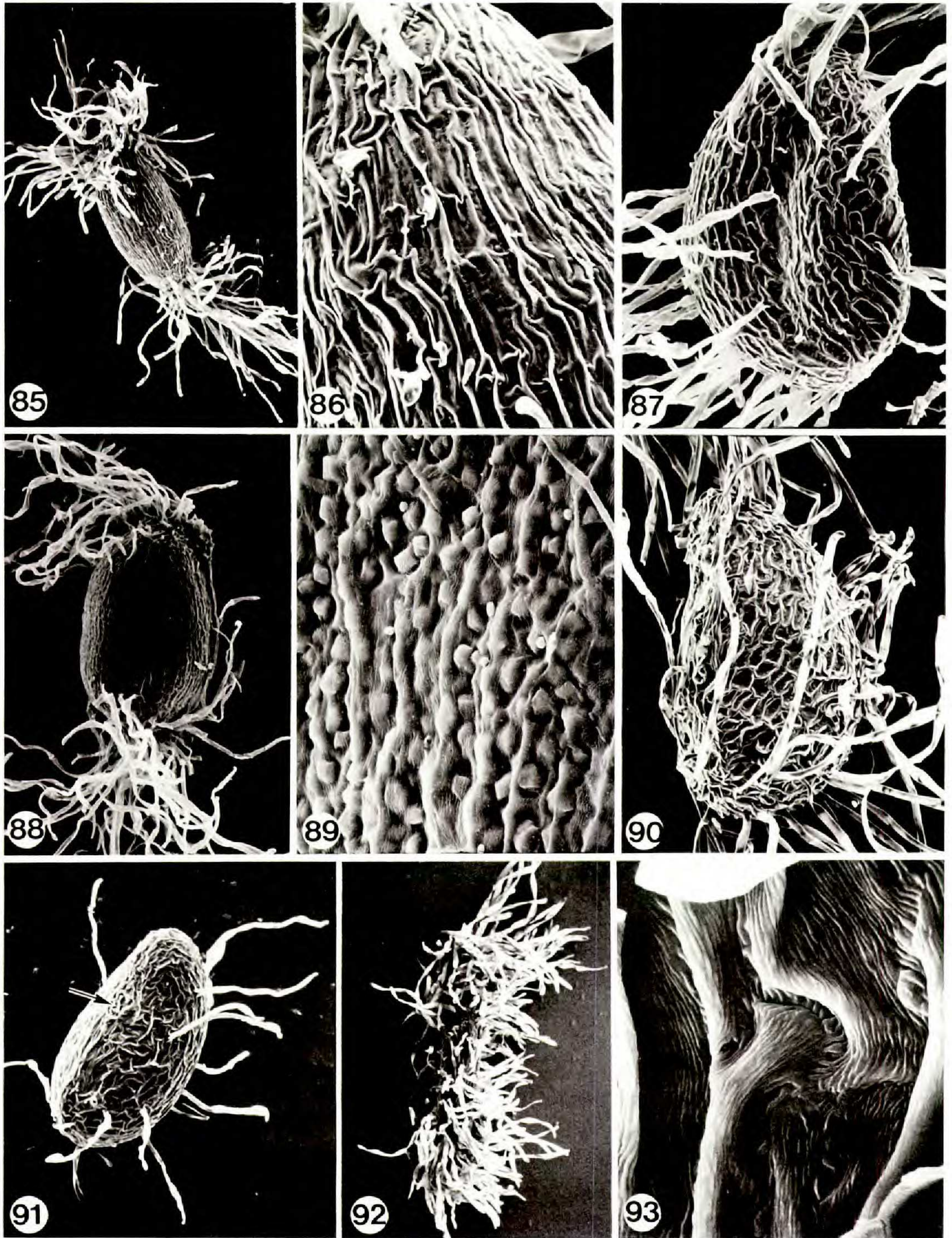


PLATE X

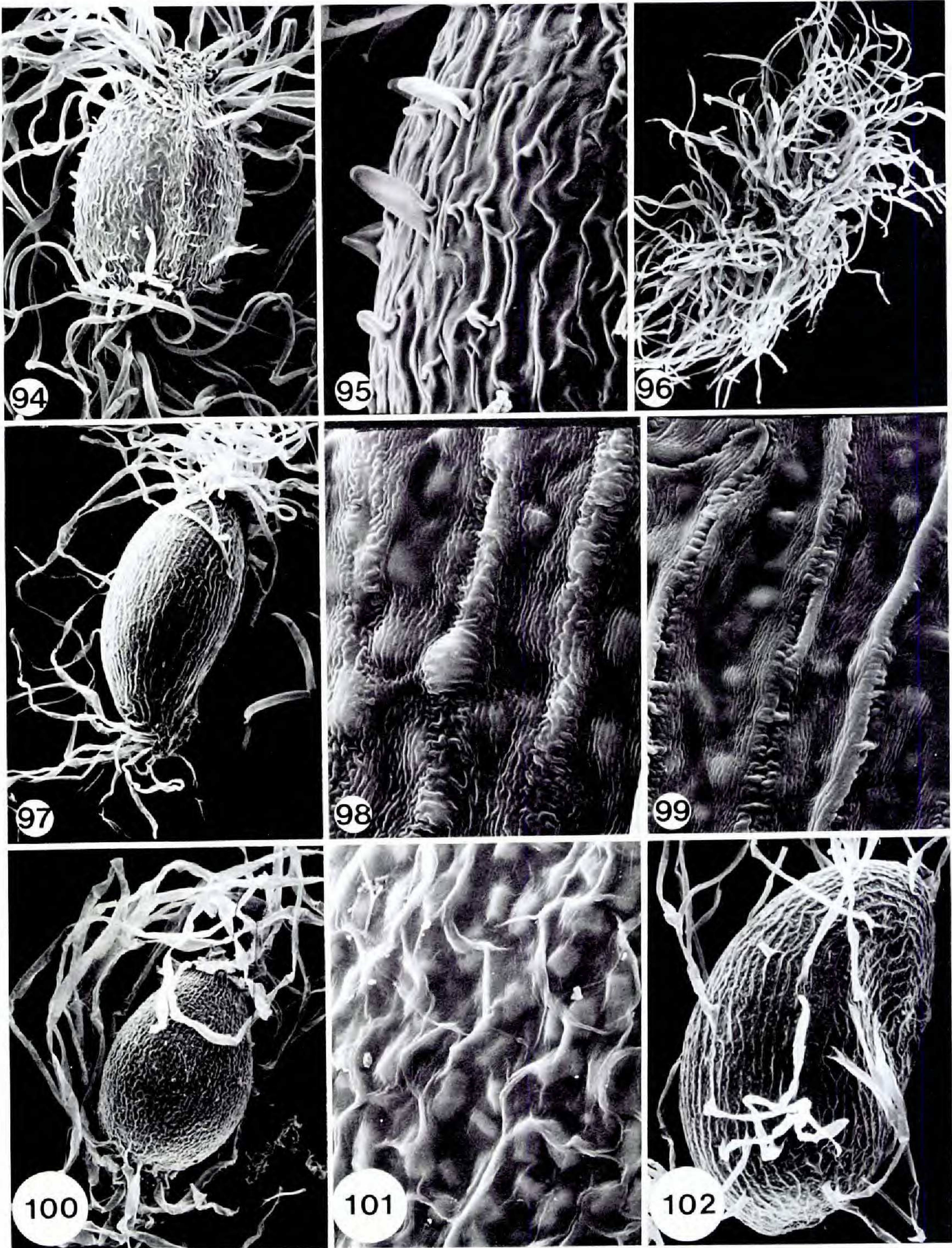


PLATE XI

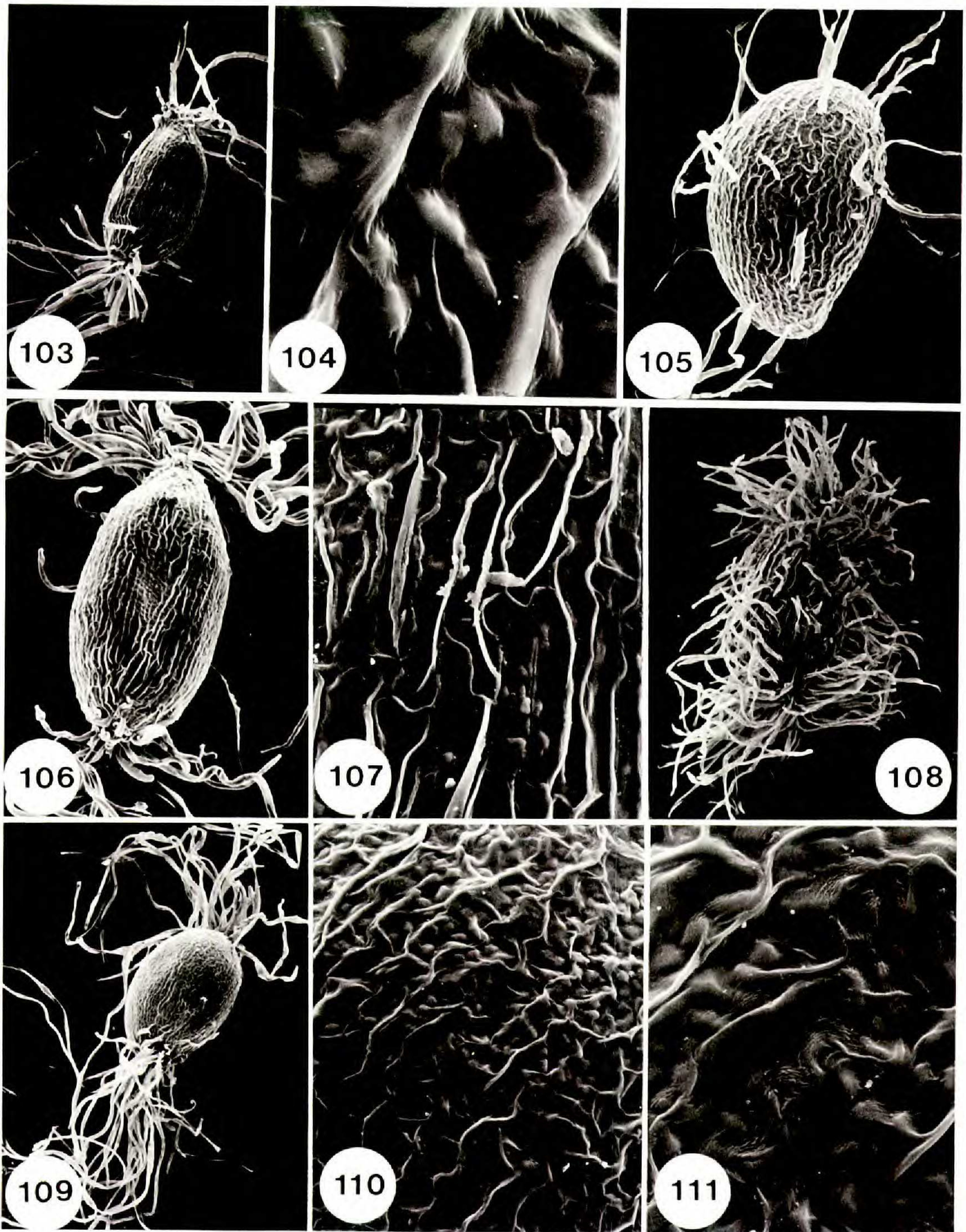


PLATE XII

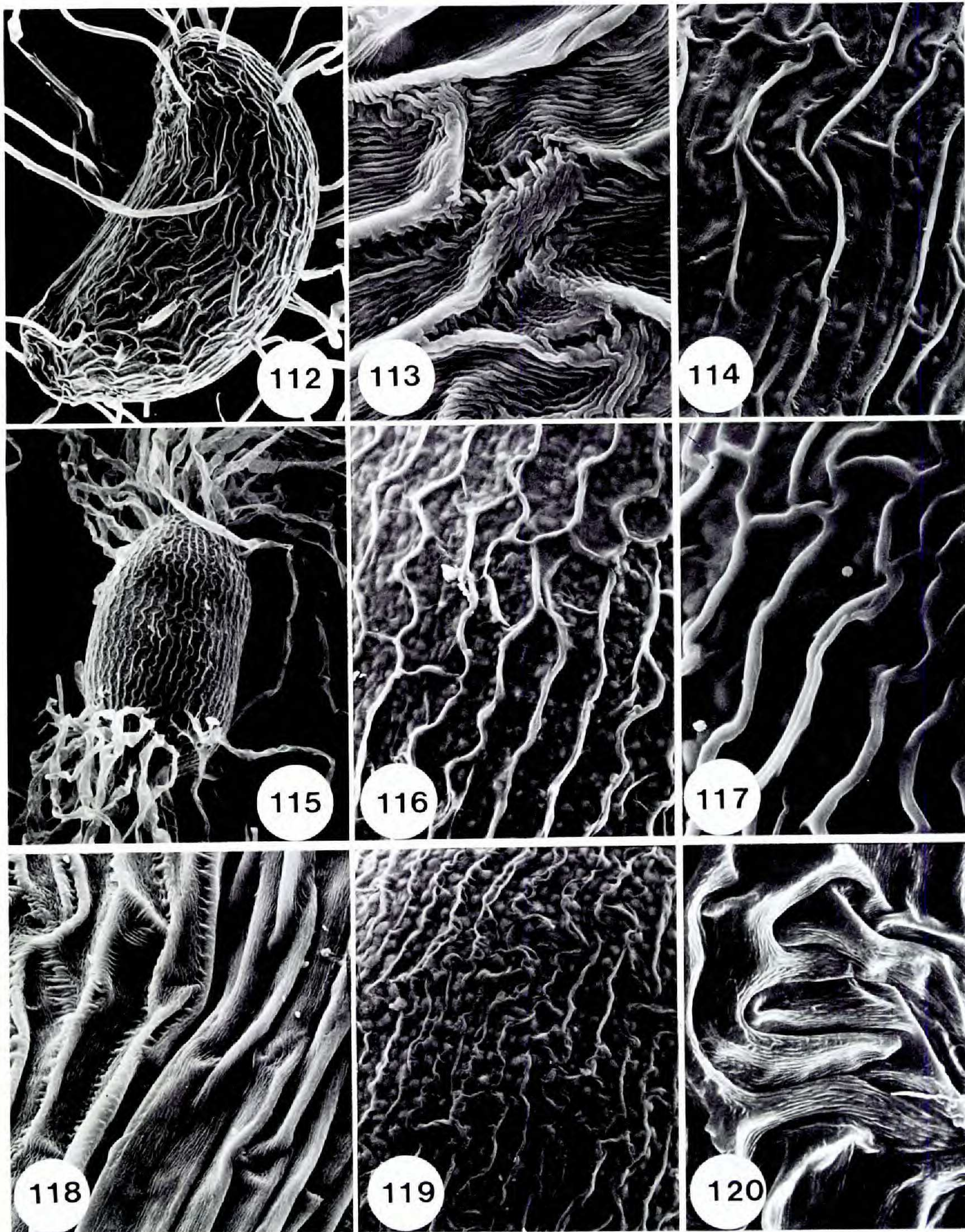


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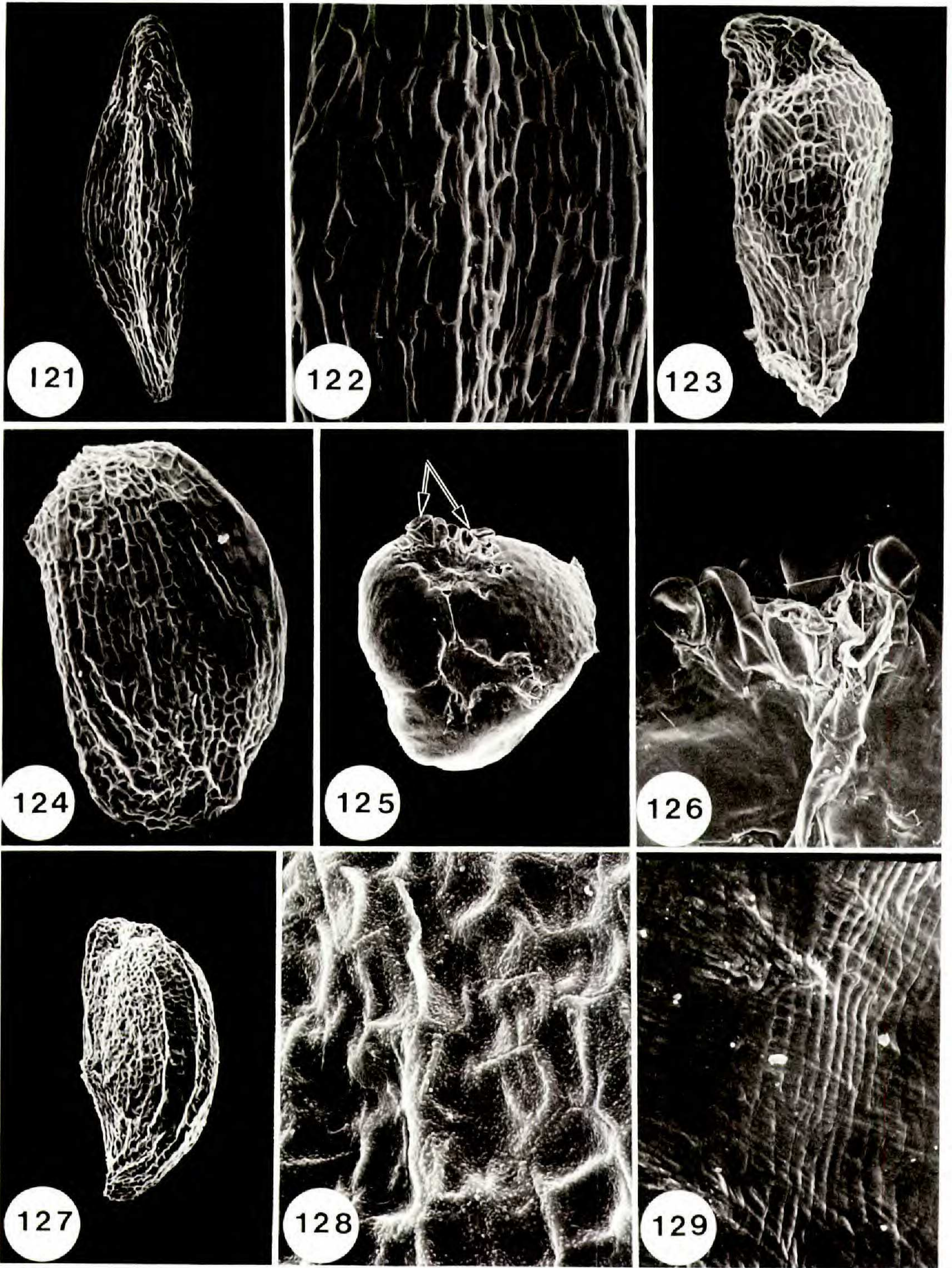


PLATE XIV



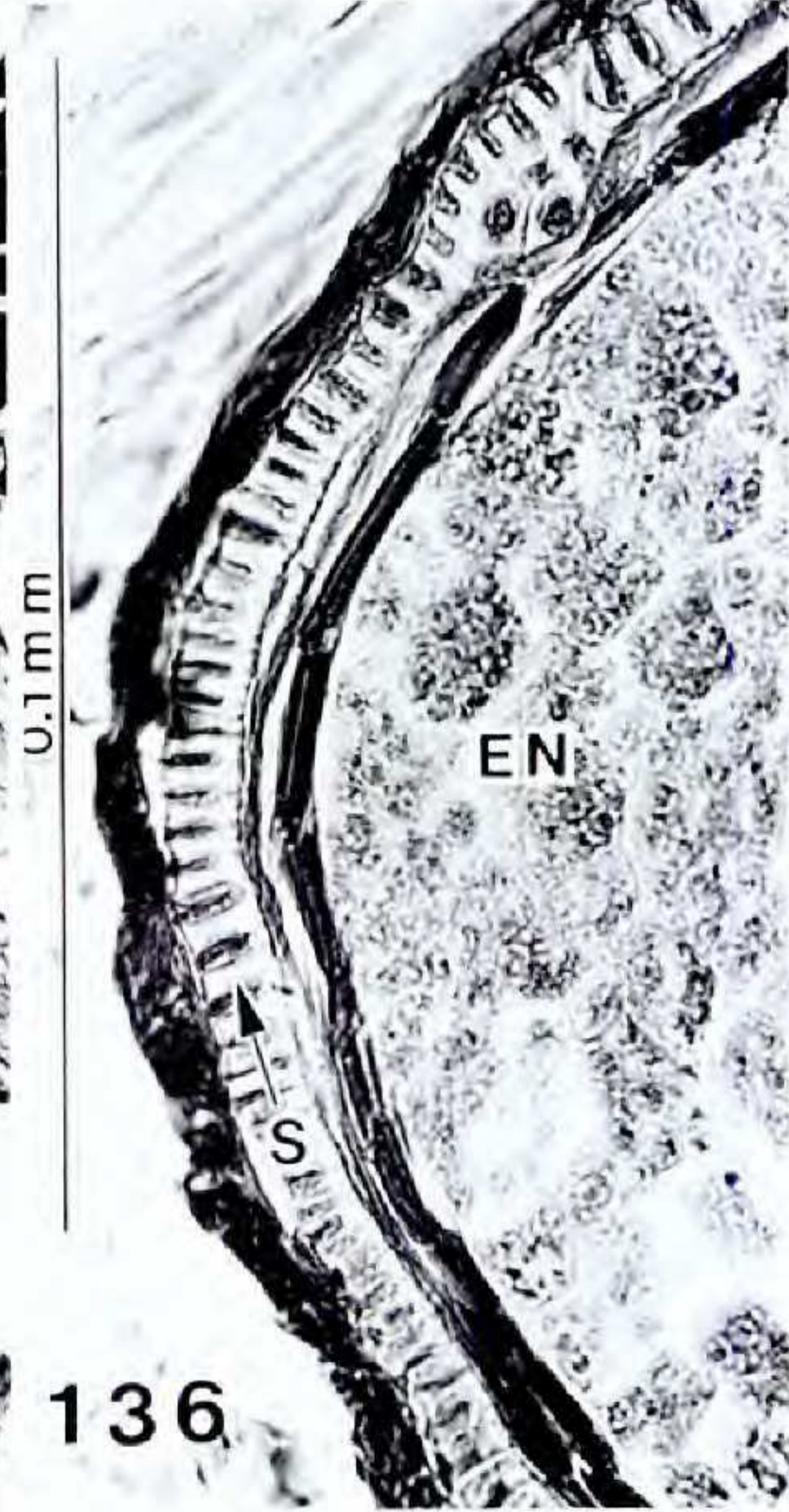
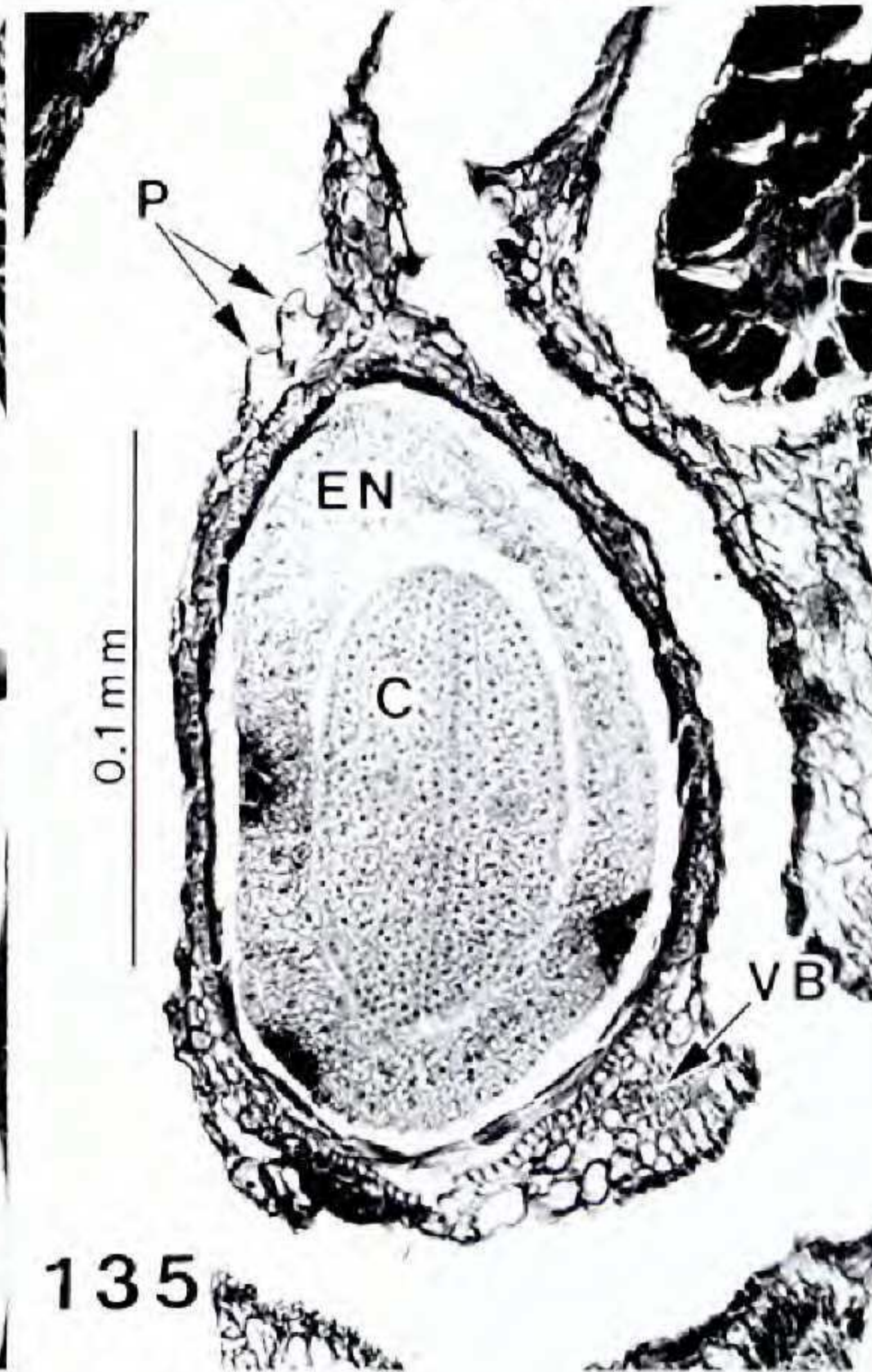
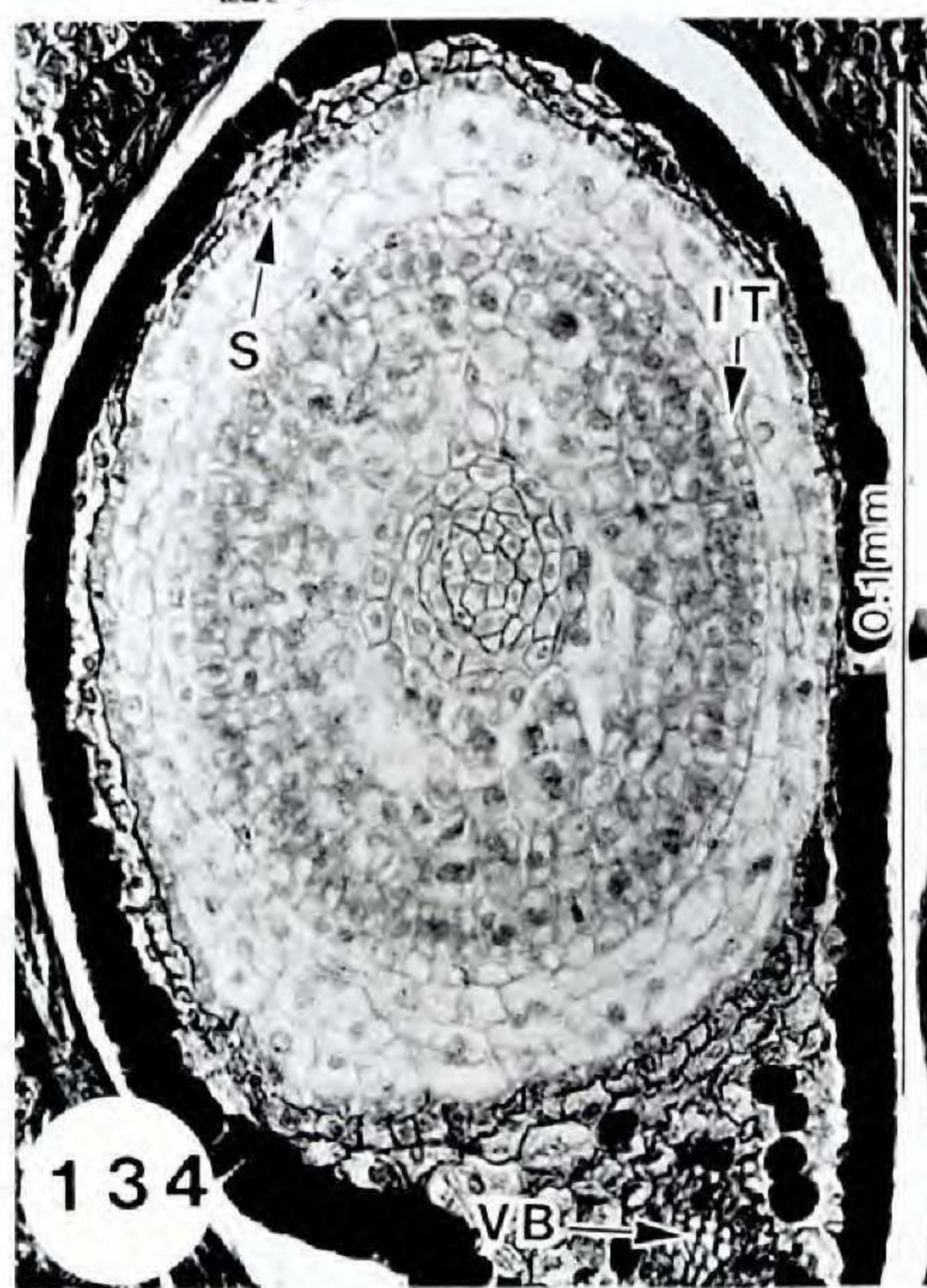
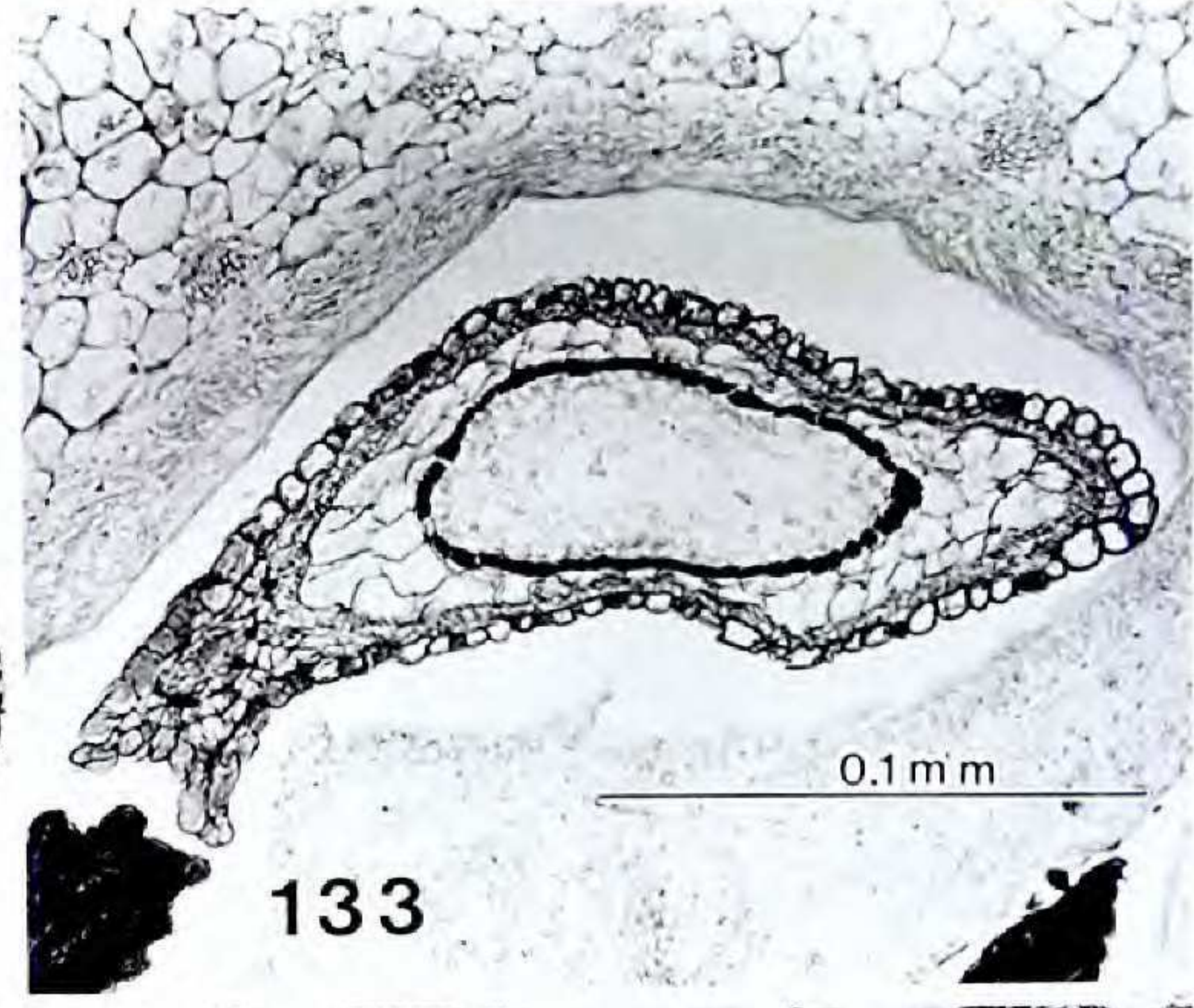
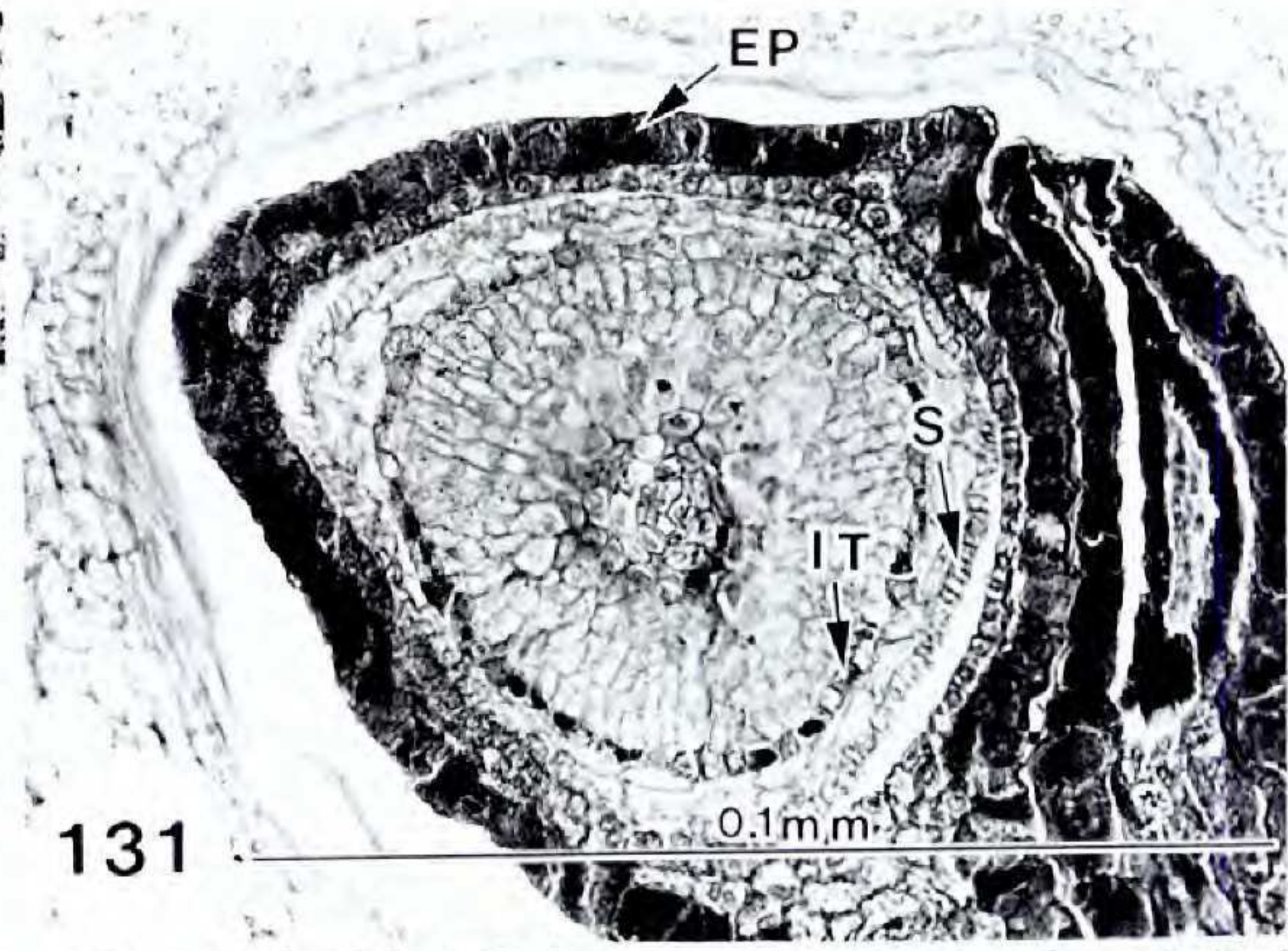
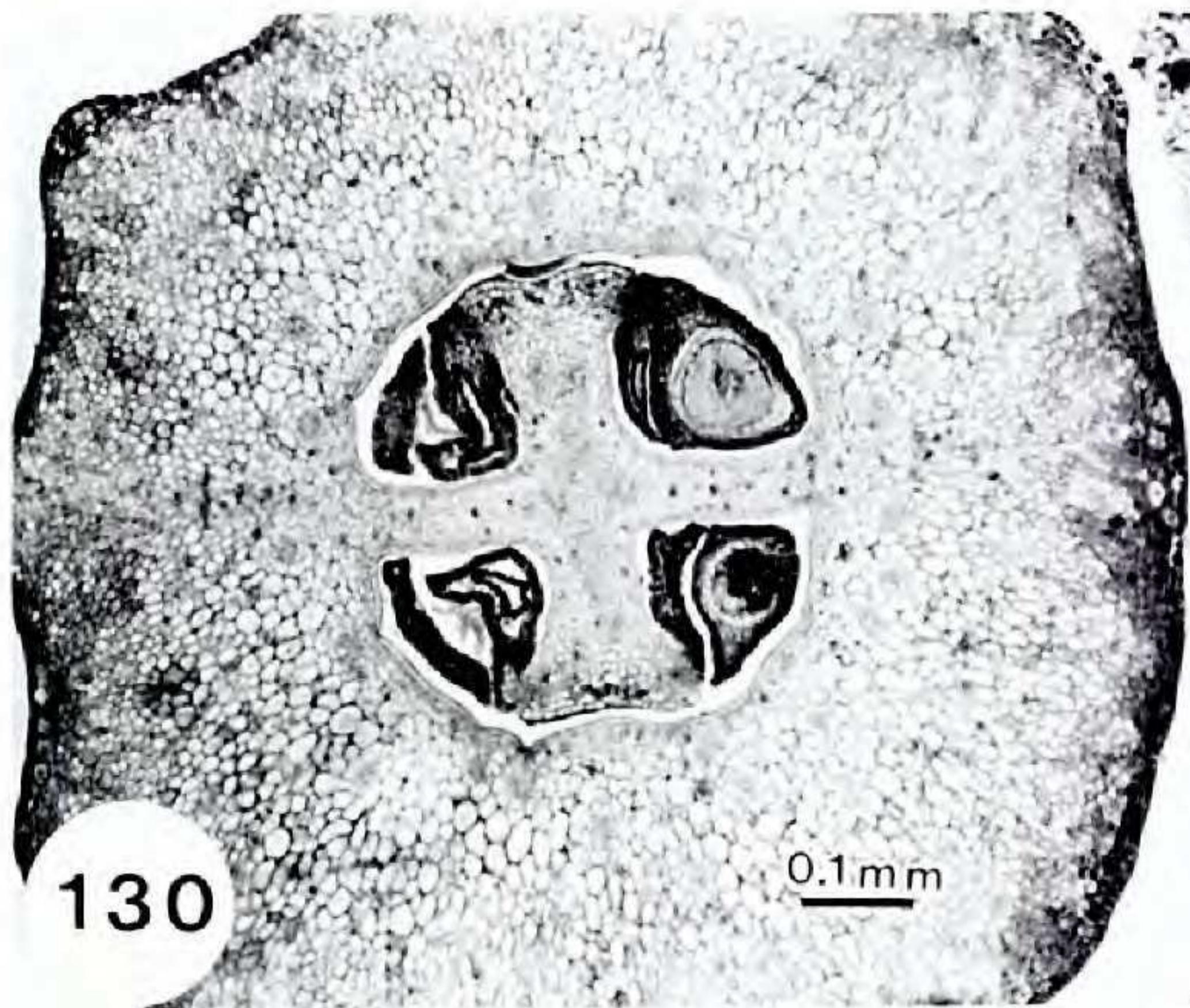


PLATE XV

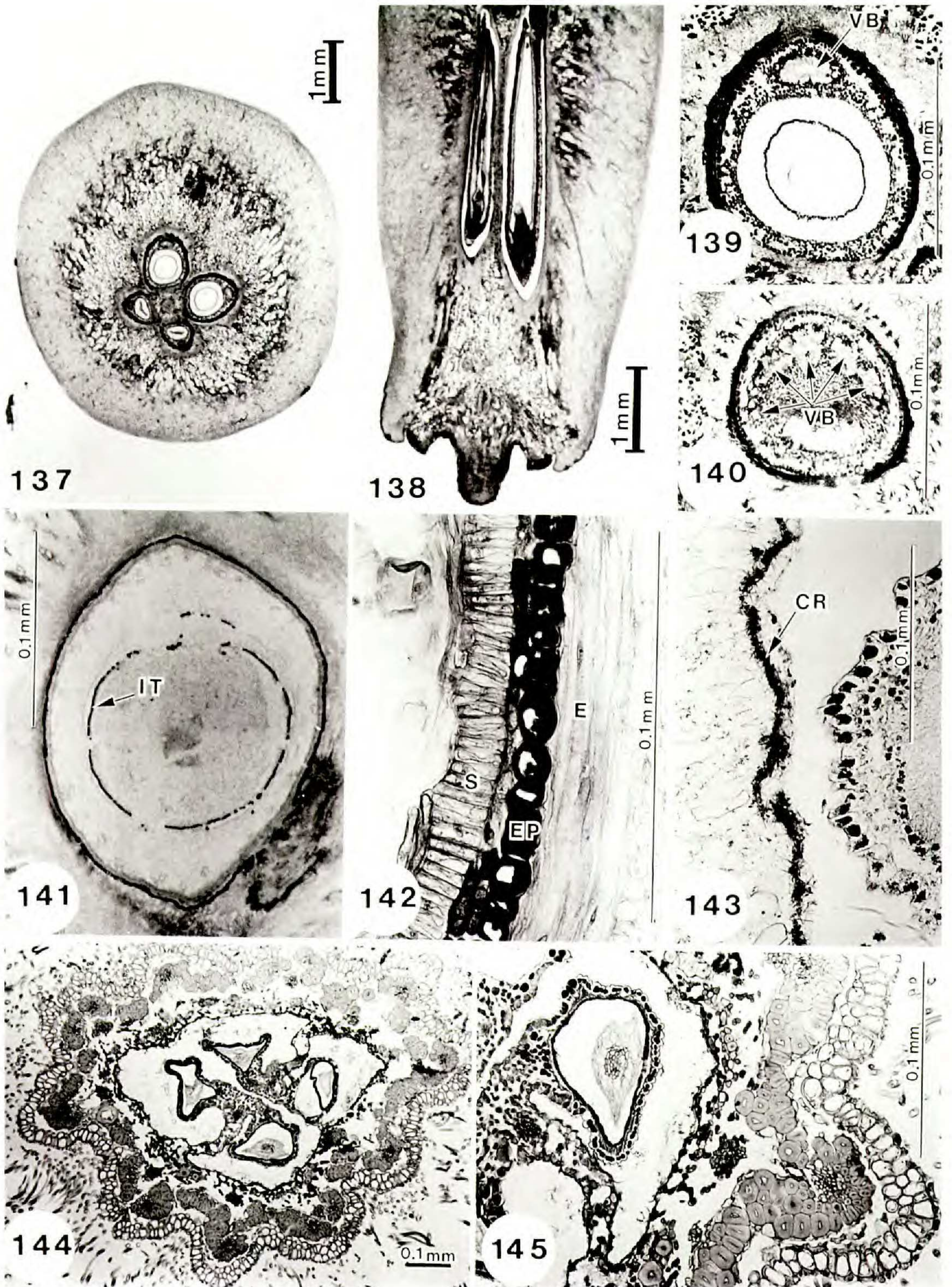


PLATE XVI